EAST AFRICAN MAMMALS

An Atlas of Evolution in Africa

Volume IIIA

Jonathan Kingdon

Academic Press
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This is the first part of the third volume of this celebrated study of the mammals of Kenya, Uganda and Tanzania. Its predecessors, Volume I on the primates and Volume II on the small mammals, have already been internationally acclaimed, and the publication in three parts of this last volume will complete what must come to be regarded as one of the most comprehensive and fascinating zoogeographical studies ever made.

Like the other volumes, this part, on the carnivores, is illustrated throughout with the author's exquisite drawings and sketches. In approaching the investigation of scientific phenomena with an artist's eye, he has achieved at once an intuitive grasp of physical beauty and character, and a precise zoological accuracy. '*The probing pencil*', he writes, '*is like the dissecting scalpel, seeking to expose relevant structures that may not be immediately obvious and are certainly hidden from the shadowy world of the camera lens.*' However, the aim is not only to illustrate the East African fauna. African wildlife is not easily separable into distinct regional varieties, and the fauna described here are representative of Africa as a whole. Nor do the descriptions and profiles of each species rest with the drawings alone. A wealth of information—including local names, breeding, measurements and food—is given; and the text encompasses forms and habits, past and present distributions, evolutionary processes, genetic changes and differences, anatomy, behaviour, ecology and the problems of conservation in East Africa. A special feature of this volume is an original analysis of the biological function of coat colours in Canids,. Viverrids and Felids, and a study of animal communication by facial expression and signal patterns.

One aim of this unusual, sensitive and brilliant work is to repair the ancient connections between man and the animals, which have enriched human culture for millenia and are now so tenuous. *East African Mammals*, both in its splendid visual impact and in the wide range of its treatment of mammalian ecology, will excite and extend the imaginations of all who read it, and help, perhaps, to halt the destruction of this complex but endangered faunal region.

£68·00

Donat Agosti
VI. 90
London

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Volume III Part A (Carnivores)

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Preface

The aim of this book is to picture a wonderful variety of animals and at the same time to provide a long overdue inventory and atlas of the mammals of East Africa.

Both the variety of mammals and their distribution are manifestations of the evolutionary process and so it is evolution that is the central theme of this book.

It is in search of further information about the process that I have essayed into the behaviour, ecology and anatomy of species. It cannot be said that the inclusion of these topics will bring the volume any nearer to being comprehensive, but they may perhaps serve to increase awareness of the magnitude and magnificence of evolution.

The book is also intended to provide a broad background for the student of East African mammals, with information on local names, breeding, measurements, food and so on. As the animals have economic, medical and veterinary importance to the East African countries and a scientific value for the world at large, I have also included some data on these aspects.

Whether one is interested in their conservation, their exploitation or their control, a practical approach towards mammals in East Africa must be based on biological knowledge and I hope this work may be found useful by all those with an interest in this fauna.

The prime stimulus for the drawings, however, has been the contemplation of physical beauty in mammals; this is a reward in itself. Drawing is the discipline in which I am trained, and it has been a chosen form of note-taking and a useful adjunct in the study of mammals. The making of a drawing is not only a matter of technique for there is a constructive effort to "figure" the animal; looking at drawings can also be an active retracing of this figuring process and it is in this that I hope others will share the pleasure of looking at animals.

East Africa is not a natural geographic or faunal region, so the fauna discussed here really belongs to a very much wider area, and in many ways is broadly representative of the fauna of Africa as a whole.

Sub-saharan Africa is occupied by the fauna of two biotic extremes, moist forests and dry open savannas (see Maps 1 and 2), and East Africa has been an ancient theatre for the excursions of these habitats and their fauna. If maps of the forest and savanna faunal zones of contemporary Africa are superimposed, the result is a broad overlapping area in central and East Africa. At the present time forest mammals are confined in this region to numerous small islands of forest, but there have undoubtedly been several periods when the forest was very much more extensive, and other periods when arid conditions were widespread. Mammal populations have therefore been subjected to isolation and gradual but extensive climatic change. On a large continent with relatively few physical barriers to the movement of animal populations, climatic fluctuations leading to the isolation of populations over millions of years have been an important determinant in the evolution of species.

The "overlap" area in central and East Africa (see the third map, p. vi)

contains many endemic species, and these forms have received particular attention in this work.

The patterns of mammalian evolution seen today have been and are being continuously modified by man. Although greatly accelerated today, human interference is nothing new, and hominid fossils testify to the continuous presence of men and pre-men in this area over millions of years.

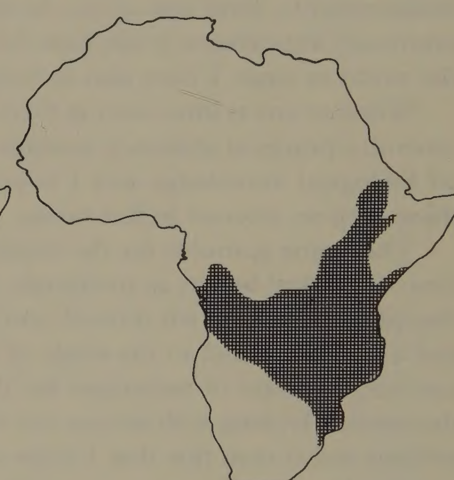
Our own emergence and survival as a species was within a rich community of mammals such as is found in East Africa today. The interaction of man and wild mammals dominated human culture for millennia, yet today the close and ancient connections with animals have long ceased to be a part of human culture. It is urgent that we gain some insight into this world that is so much a part of our inheritance and so much older than our civilization which is destroying it.

Area in which forest mammals recorded
Forest area at present
Desert foci

typical species:–
Nandinia binotata
Cephalophus
Neotragus spp.
Anomalurus spp.
Helioscuirus spp.
Dendrohyrax

Area of distribution of savanna mammals

typical species:–
Galago senegalensis
Lycaon
Hystrix
Procavia
Diceros
Giraffa
Phacochoerus
Many spp. of antelopes



Overlap zone of forest – savanna fauna

Contents

KEYS

Carnivores

Carnivora
- **Canidae**
- **Mustelidae**
- **Viverridae**
- **Hyaenidae**
- **Felidae**

Of the many ways of measuring a land's wealth one of the surest signs of ecological richness and diversity is an abundance of predator species.

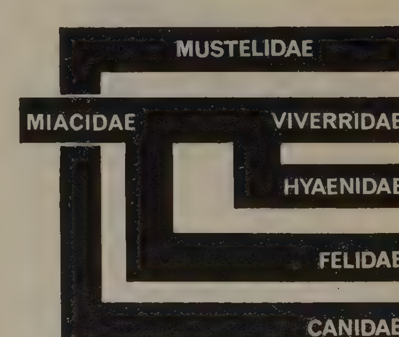
Because each species sits at the top of a different food chain, belonging to a different cycle of organic matter we can be certain of the existence of a larger animal community for every predator. This is in turn sustained by vegetation. The existence of carnivores carries the implications of a larger ecological community and of millions of years of evolutionary struggle. Each has seized for itself a very precise and measurable share of animal matter which it can only acquire under quite specific and limited conditions.

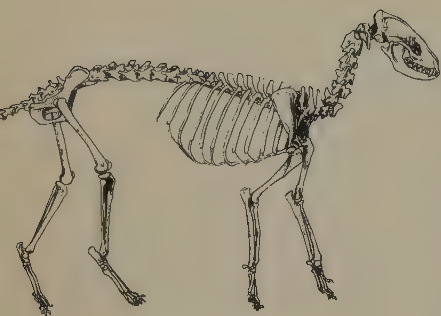
In every habitat mammalian carnivores exploit a large part of the available animal protein. Insects and birds probably consume more but the carnivores are impressive for the range of habitats they have invaded and for the strategies they have evolved to overcome the difficulties posed by a multitude of different types of prey.

There are forty or more species of carnivores in East Africa alone and the homogeneity of the Carnivora is difficult to appreciate because of the diversity of their adaptations. A poor fossil record in East Africa does little to illuminate their evolutionary background. However, many facets of the evolutionary radiation of the Order can be illustrated by reference to the living species. In the broadest sense, both the resources that sustained the earliest carnivores and their habitats continue to exist today and many of the contemporary species can be described as occupying ancient carnivore niches. That some of these may be extraordinarily exacting is shown by convergence between carnivores of quite different stocks, for example, several of the American procyonids have viverrid equivalents in Africa, as do some of the Eurasian mustelids.

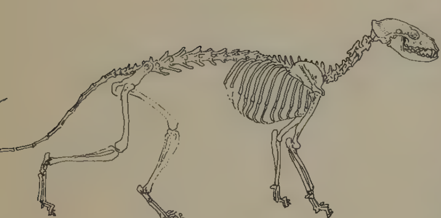
From our knowledge of fossil Miacidae outside Africa we know that this family was ancestral to all modern carnivores. So closely do these animals resemble viverrids that some authorities (following Gregory and Hellman, 1939) have suggested that the viverrids are nothing more than advanced miacids which could actually be united in a single family. The taxonomic situation is succinctly summed up by Simpson (1945).

> "The Miacidae resemble the Viverridae in many ways and are almost perfectly prototypal for them, but without apparent exception the resemblances are in characters primitive for all fissipeds including the canoids. Studying the Miacidae in connection with the Canidae, rather than the Viverridae, would justify placing them in the Canidae on the same basis and this has, in fact, been done. Placing them in the Viverridae is nearly equivalent to saying that the Canidae were derived from the Viverridae. Such definitions are legitimate and given these definitions this sequence and its taxonomic expression are valid. Nevertheless, the Miacidae are diagnostically distinguishable from Viverridae and Canidae and prototypal for both."





Civet cat (*Civettictis civetta*)



Oligocene carnivore (*Pseudocynodictis*)

In spite of taxonomic objections to regarding Viverridae and Miacidae as synonymous our imaginative grasp of carnivore evolution is aided by recognizing that the viverrids are both conservative and versatile (which canids are not) and as a group they depart least from the generalized carnivore prototype. (Indeed, some of the viverrids can even exemplify mammals as a whole and it was with this in mind that I chose the civet to illustrate the notes on mammalian anatomy in Vol. I, pp. 95—97.)

In the Palaeocene and Eocene fossil beds of Eurasia and North America and from the Eocene to the Miocene in Africa, the dominant carnivores to be preserved are the primitive Creodonts, which were often of gigantic size and exhibited peculiar specializations. It was in the context of the Creodonts' dominance that the Miacidae slowly emerged as apparently larger brained animals in which the carnassial teeth developed at the front rather than the back of the toothrow. They were generally of smaller size. MacIntyre (1966) has suggested that there were insectivorous, specialized predatory, somewhat omnivorous and arboreal forms.

The development of the large-brained primates from an arboreal insectivore might be echoed here in that brain development is linked with the co-ordination, dexterity and agility that are required for life in the trees. An arboreal existence also puts limits on size. In spite of forests having been very extensive before the Miocene, small animals from this habitat are generally poorly represented as fossils and Ewer (1973) has suggested that this may explain the rarity of fossil miacids.

I discuss some aspects of the relatively recent radiation of African viverrids in the profile of that group and in the text on individual species. Returning to the idea of living carnivore fauna as an evolutionary array, it is possible to regard the palm civet as the contemporary equivalent of an arboreal miacid, while the genets and civets represent arboreal and terrestrial offshoots. So cat-like is the genet that we can easily envisage the development of felids from such a creature.

The felids are graduated in size from wild cat to lion and this can be viewed both as an evolutionary trend towards greater size and as an ecological radiation into niches which are related to the size of prey animals and their habitats.

The hyaenas developed directly from an ancestral viverrid which would have some resemblance with the living civet. The long limb proportions, greater size and emphasis on carnassial shear in the teeth are also characteristic of the Canidae but this family diverged very much earlier from an ancestor that MacIntyre (1966) identifies quite specifically as *Miacis*. Both these families have adapted to open country and speedy gaits. The possibility that they have interacted in the past is discussed in the hyaenid profile.

The mustelids' divergence is about as old as that of the canids and both branches would seem to have seen their principal radiation outside Africa. The wide range of mustelids in temperate Eurasia and America can be matched by that of the viverrids in the Old World tropics, but the former are undoubtedly more highly specialized as predacious killers, and there is the implication that this is of greater advantage in the north, where winter diets do not allow for any buffering from insects, fruit or other foods, which are commonly eaten by the more opportunistic mongooses.

The co-existence of only a few mustelid species with a large variety of

viverrids in Africa suggests that the former are only able to compete in a limited number of highly specialized niches.

Competition looms large in the lives and evolution of carnivores. It exists at every level, between different individuals and classes of the same species, between species or families and between carnivores and other animals, including reptiles, birds and insects. Its role in the past has clearly influenced which predators should dominate the scene in different habitats, continents or periods of time.

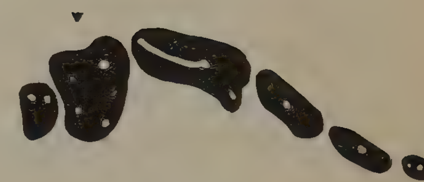
The progressive replacement of the creodonts (hyaenodonts) by modern carnivores was later in Africa than elsewhere (see Vol. I, p. 55). Cooke (1963) and Savage (in press) and the fossil record show that the contemporary large carnivores have replaced the earlier Pleistocene fauna in which sabre-tooths and a number of hyaena species flourished. The species known from East African sites are listed on p. 255. The fossil carnivores of Africa are discussed in Savage (in press) and a general account of the order's palaeontology is available in Romer (1966, i.e., revised edition).

A major influence in the evolution of large predators has been the continuous evolution of their prey. In the course of competing amongst themselves, feeding efficiency is not the only consideration for herbivores; those that are more vulnerable generally give way to those that are less so. Within any single lineage there is also a tendency for the evolution of larger species. As its size increases, the herbivore becomes vulnerable to fewer species of predators and various advances in the social life of bovids constitute improvements in their defences against predators. Because of this it is possible that some of the large extinct carnivores were unable to switch on to these prey species as older forms declined. Since predators in turn evolve by matching their prey's advances with better techniques for getting them, there is a continuous interaction between predator and prey, prey and predator. As a result the dominant large carnivores of the present day are probably distinguishable from extinct species by a versatility, speed and hunting efficiency that is the end product of ceaseless competition.

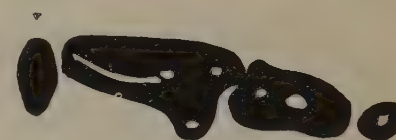
Three distinguished workers, Schaller, Kruuk and Kuhme have demonstrated that the major social predators, lions, hyaenas and wild dogs have evolved sophisticated social mechanisms which serve to improve their hunting success and the survival of their species.

When different populations of the same species have been compared, as Kruuk has done for hyaenas and Schaller for lions, differences sometimes appear that are highly significant for our understanding of relationships between the environment, competition and social organization. Hyaenas that are able to live at the highest densities actually regulate their prey's numbers and establish an equilibrium between predator and prey, which is not found in areas where the numbers of either are subject to sudden change. Because hyaenas consume their prey very fast, there is little waste for late-comers in high density habitats and there is a premium on every animal being in on a kill. Since the tight social units of hyaena "clans" found in the Ngorongoro crater make it possible for its members to hunt larger and more difficult prey, the diminished chances of survival for hyaenas that are slow to join the clan automatically reinforce the value of social hunting and the associated behaviour. In this species competition for food centres on the speed with

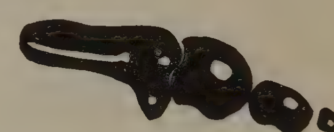
TEETH



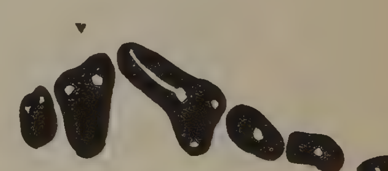
Canid



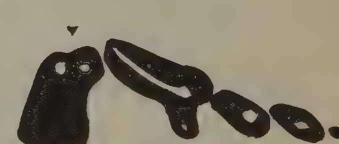
Felid



Hyaenid



Viverrid



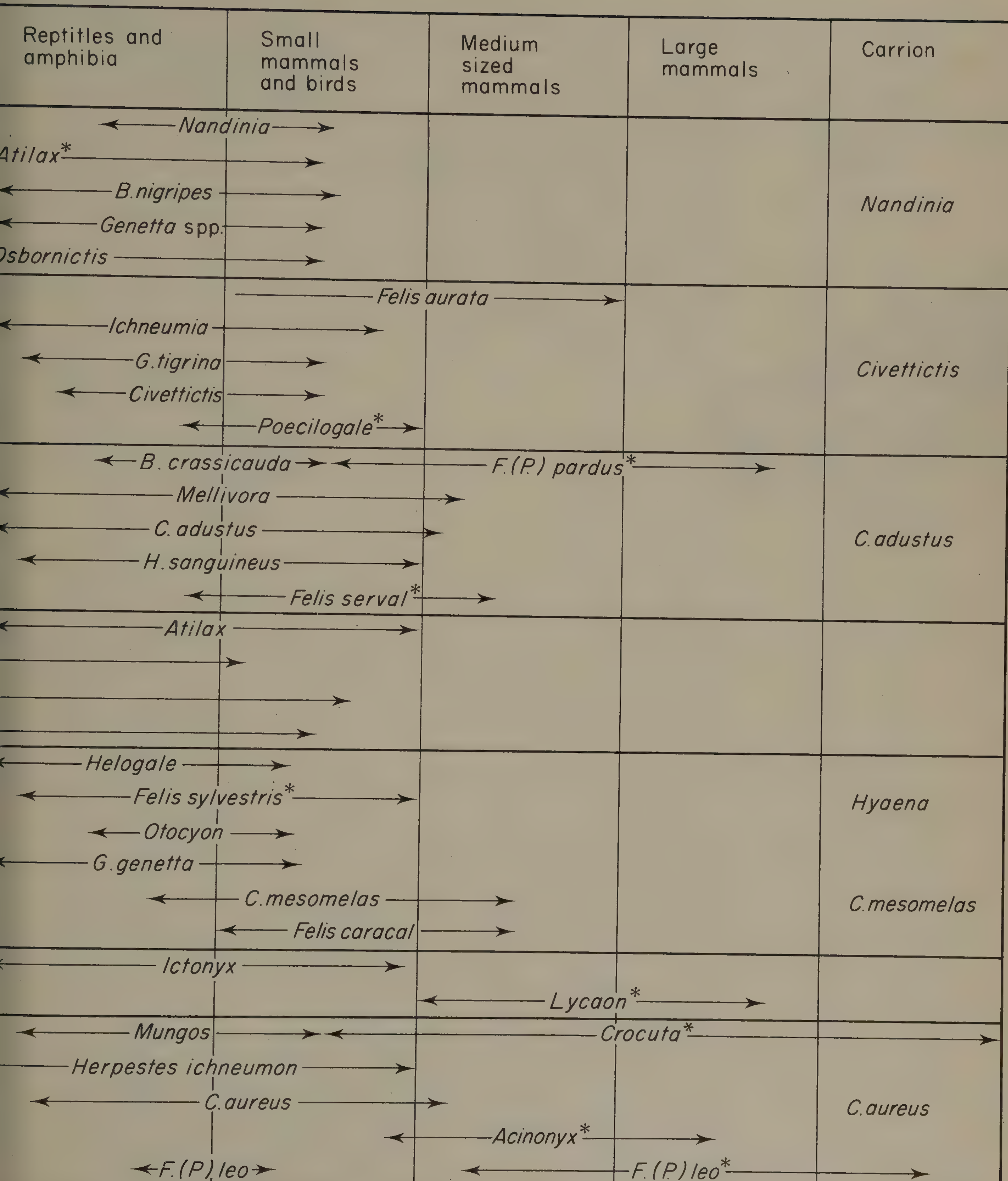
Mustelid

CARNIVORE

Habitat	Fruits	Sessil or cryptic invertebrates and eggs	Active invertebrates	Aquatic or semi-aquatic fauna
Forest		*Nandinia* *Crossarchus* *Bdeogale nigripes* *Genetta servalina* *Genetta victoriae*		
Secondary growth		*Dologale* *Ichneumia** *Genetta tigrina** *Civettictis** *Rhynchogale*		
Moist savannas and Woodlands		*Bdeogale crassicauda* *Mellivora** *Canis adustus** *Herpestes sanguineus**		
Marshes and aquatic		*Atilax** *Aonyx* (*Paraonyx*) (forest swamps and rivers) *Aonyx* (*Aonyx*) (swamps and rivers) *Lutra* (rivers and lakes)		
Thickets dry savannas and woodlands		*Helogale** *Hyaena* *Otocyon* *Genetta genetta* *Canis mesomelas*		
(Interzones)		*Ictonyx** *Proteles**		
Grasslands		*Mungos** *H. ichneumon** *Canis aureus*		

Species marked occupy a wider range of habitats than can be suggested in a simplified table

NICHES



Reptiles and amphibia
Small mammals and birds
Medium sized mammals
Large mammals
Carrion
Nandinia
Atilax*
B.nigripes
Genetta spp.
Osbornictis
Nandinia
Felis aurata
Ichneumia
G.tigrina
Civettictis
Poecilogale*
Civettictis
B. crassicauda
F.(P.) pardus*
Mellivora
C. adustus
H.sanguineus
Felis serval*
C.adustus
Atilax
Helogale
Felis sylvestris*
Otocyon
G.genetta
C.mesomelas
Felis caracal
Hyaena
C.mesomelas
Ictonyx
Lycaon*
Mungos
Crocuta*
Herpestes ichneumon
C.aureus
Acinonyx*
F.(P.) leo
F.(P.) leo*
C.aureus

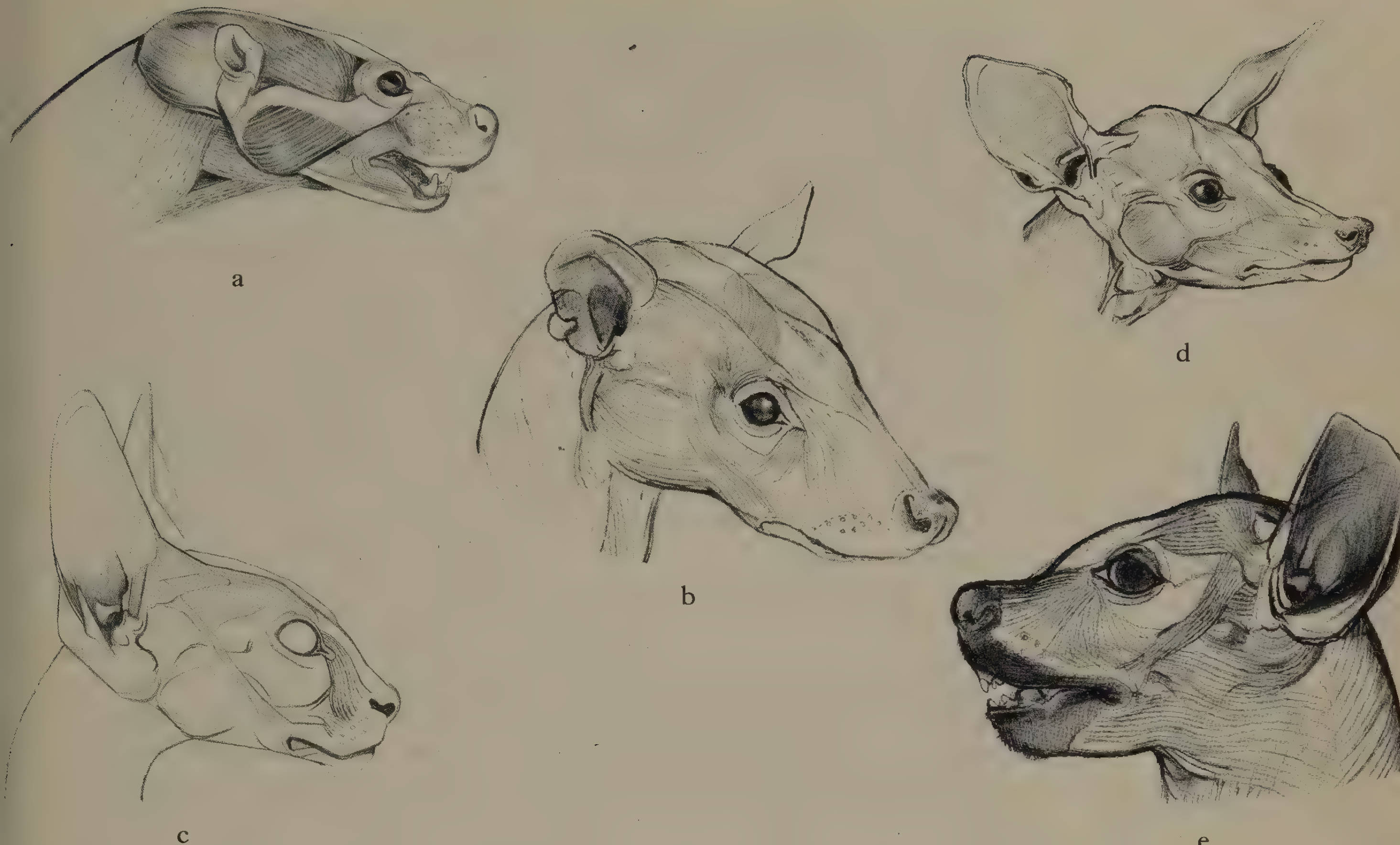
which it can be torn apart and swallowed. Lions, instead, settle their priorities in favour of the largest males through threats and fighting.

The profiles that follow contain numerous examples of competition both between and within species. Nonetheless, competition between species is generally minimized by differences in the bulk and type of food and by the methods of finding, catching and killing it. Habitat preferences, activity patterns and differing responses towards seasonal changes in their foods also separate carnivores. Occasionally these divisions correspond with family differences; for example, no African canid or hyaenid lives in true forest, all living hyaenas are nocturnal and all viverrids have diminutive prey and are relatively small themselves. The chart on pp. 4 and 5 summarizes the separation of species according to habitat and type of food.

A major consideration with numerous implications for the anatomy and social organization of the carnivores is the mechanism of getting food. Canids run it down by sight, track it by scent or listen for it. Felids generally find their prey by sight and then stalk or ambush from cover and the mustelids and mongooses use sight, scent and touch to find their food. Killing methods are rather distinctive; felids and mustelids tend to make well-aimed bites at the neck or throat and kill by dislocation of the vertebrae or suffocation. Canids and hyaenas are often less accurate, killing through persistence and worrying. Viverrids are very varied, their feeding methods being adapted to the characteristics of their food. There are considerable differences in the speed with which they eat, according to the agility of their prey or the competition they can expect from their fellows. It is often difficult to judge the relative importance of a sense in hunting behaviour and this is even more true for social behaviour but the accompanying table of sensory priorities may help to illustrate in a crude way this facet of their specialization. Together with limb proportions and body size, the relative sizes of ears, eyes and muzzles provide physical evidence of divergence both at the level of the family and below. Small changes in the relative importance of a sensory organ alter the characteristic shape of a head and skull and we can readily appreciate the remarkable transformations wrought by evolution by comparing heads and skulls (see opposite). Such comparisons illustrate the conservative and unspecialized nature of the viverrids in respect of other carnivore families.

Carnivores have a variety of scent glands, some have anal and perineal sacs, others have secretions between their toes or localized areas of skin containing specially modified cells producing secretions. Dung, urine, sweat and saliva are all used for communication and it is difficult to overstress the importance of scent for the spacing of individuals and for the social and sexual behaviour of all species. Much of the significance of scents is hidden from us but the timing of sexual activity sometimes coincides with greater activity in anal and other glands (Spannhoff, 1969) and it is clear that information on status and condition is conveyed in the anal scent of dogs and other carnivores, leading to attraction or avoidance by conspecifics.

In the zorilla and some other mustelids, glands have been specially modified to secrete and squirt nauseous secretions that deter larger predators. The honey badger has modified this technique to deter and disable bees when it attacks a hive. Vocal communication is most highly developed and frequent in the social carnivores, particularly mongooses but almost all



a. Mustelid (*Lutra maculicollis*) b. Viverrid (*Civettictis civetta*) c. Felid (*Felis serval*) d. Canid (*Canis adustus*)
e. Hyaenid (*Crocuta crocuta*)

		Scent	Hearing	Vision	Touch
CANIDS					
	Jackals	1	2	2	-
	Bat-eared Fox	2	1	3	-
	Lycaon	3	2	1	-
MUSTELIDS					
	Mustelines	1	3	2	3
	Otters	2	3	1	1
VIVERRIDS					
	Atilax	2	4	3	1
	Mongooses	1	3	2	-
	Genets	3	2	1	-
HYAENIDS					
	Hyaenas	1	2	1	-
	Proteles	2	1	3	-
FELIDS					
	Felis spp.	3	2	1	-
	F. serval	3	1	2	3

species employ contact, threat or alarm calls at appropriate times.

Bodies, tails, ears and faces move with an expressiveness that is only rivalled by the primates and visual communication is highly developed in many carnivores. In the individual profiles I have discussed examples of visual signalling and noted some of the devices which distract attention from the head to the genitalia, and some representative coat colours and signal patterns are discussed.

There is also the phenomenon of melanism, which occurs with some frequency in several felid and viverrid families and is unknown in others. In every case it occurs primarily in nocturnal species with elaborately camouflaged coats and in areas where the carnivore is reasonably abundant. Could there be hidden advantages in melanism for it to be relatively frequent only in certain species and in certain localities? Species that are already well camouflaged are unlikely to gain any advantage at night by being black. Their greater conspicuousness by day should be a hindrance, but it is conceivable that there might be some unknown benefit. For the majority of species that show it, melanism effectively "blacks out" an elaborately detailed system of visual signals. Postures still communicate to conspecifics but the obliteration of some of the details of a sophisticated signal system might explain why melanism occurs in some groups and not in others. If a well-established repertoire in their behaviour becomes disadvantageous under certain conditions, the cancellation of certain associated signals through "blacking out" might be one way of overcoming the disadvantage. I am unable to suggest what these conditions might be, nor guess at the disadvantages but it might be worth investigating populations prone to melanism with this hypothesis in mind. Such a drastic transformation of appearance in carnivores that are normally dependent on hiding can only occur with any frequency in habitats where the need for crypsis is not critical. Even if a local population is more wholly nocturnal and melanism actually serves crypsis it would still prejudice social signalling. If there are conditions under which blackness confers advantages that override those of detailed and highly specific coat patterns it would be worthwhile attempting to correlate frequencies in the occurrence of melanism with various ecological and social factors. Such an investigation could be relevant not only for melanism in carnivores but for the relationship between monochromatic colouring and visual communication in other groups of animals.

The carnivores are mostly solitary hunters and foragers but certain mongoose species, otters, wild dogs, hyaenas and lions have become social. In the larger species and otters this behaviour appears to be connected with greater success in hunting. In the smaller mongooses it appears to be related to greater immunity from predators by increasing the numbers of alert eyes, ears and noses. In the case of the dwarf mongoose, there is actually an age-class caste of sentries and the mechanisms whereby three or four species in the predominantly solitary Viverridae have become social are of the greatest interest.

The spacing out of solitary species in territories and the existence of hierarchies and group territories in social species are discussed in the profiles. In many species it is established patterns of land tenure rather than the relative density of prey that determines the area used by a carnivore or its

group, but Schaller (1972b) has suggested that the total range used by lions during a year represents the minimum amount of space the animals need to survive during periods of the greatest shortage and that ranges may take account of fluctuations in numbers. This is likely to apply to many other species as well.

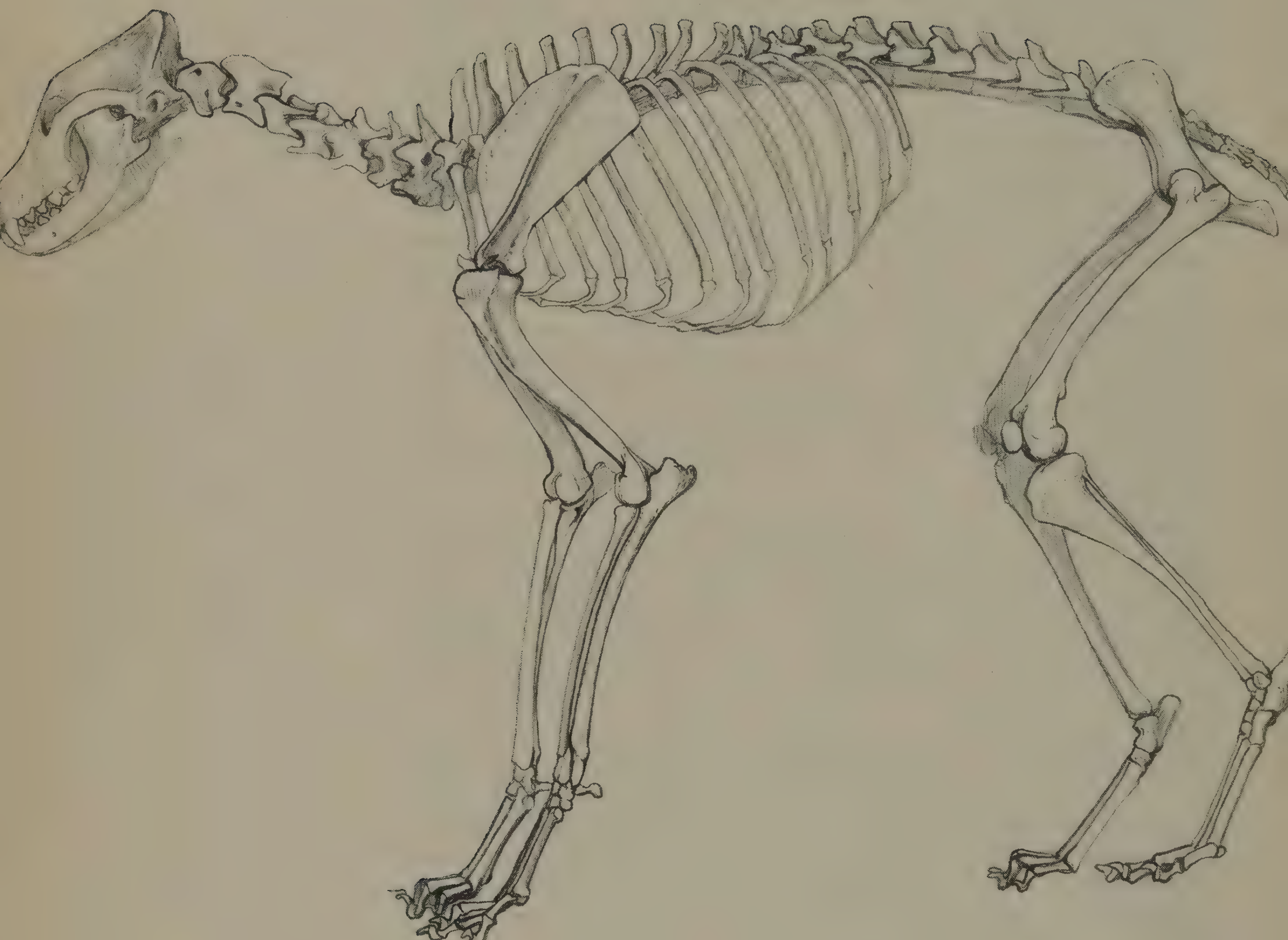
No carnivore has truly precocious young and most species require a fairly long period of learning before they are capable of fending for themselves. Most young carnivores spend long periods playing and there has been much discussion of the significance of playing. The activity obviously burns off excess energy but Schaller (1972b) has suggested it may also bond members of a lion pride and, more important, that it may help to integrate inborn motor patterns into complex functional units. It might also allow different combinations and recombinations of these motor patterns so that versatility and adaptability to a variety of circumstances can be acquired in the process of maturing. Most games involve the motions of stalking, chasing or searching, pouncing, grabbing and pulling and also threats, retreats and sexual elements that are typical of intraspecific behaviour.

A general review of the carnivores is available in Ewer (1973), who treats a number of African species in some detail as well as placing them in a broader world-wide perspective.

As I pointed out at the beginning of this discussion, the carnivores are some measure of the wealth of a region. In contrast, there are ever increasing areas of the world (including parts of East Africa) where only a few jackals or weasels pick a living in the wastelands of man's making. The emnity of man and carnivore is ancient and is due to direct competition, because we too sit at the top of a food pyramid which is an increasingly simple and artificial one.

What do we look like when viewed as intolerant predators using a new technology to set up increasingly large and artificial food pyramids to support our expanding numbers? Our activity is changing the landscape of the continents more profoundly in this century than in the last ten million years. In a gigantic effort to keep the ever increasing volume of human stomachs full, we are putting new areas under the plough every year and we spread vast fields of crops across the land, our cattle, sheep and goats steadily increase.

As we are forced to pass more and more of the world's available nutrients along our own collective gut we are displacing organic systems the complexity of which we have only just begun to appreciate. Even if our actions must be ruled by the dictates of a trillion human stomachs it is of practical importance for us to know how organic material is cycled through a succession of animal bodies, most particularly in the varied and complex conditions of tropical Africa. No natural habitat is complete without its predators (which in many instances function as regulators within the ecosystem). Is the complexity of tropical ecology a challenge to the human mind, to our curiosity and search for understanding? Or is it a challenge to the needs of the human stomach, an obstacle to be overcome with the help of technology? Depending on the answer, Africa's carnivores are all of significant interest or all vermin.



Lycaon skeleton

Canids

Canidae

Genera

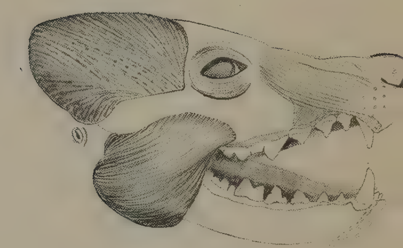
Canis
Lycaon
Otocyon

The dog family is distinguished from other carnivores by its relatively long-legged and long-faced proportions and its pre-eminence in more open habitats where it can outpace any of its other carnivore competitors.

To imagine what sorts of developments were necessary to transform an arboreal miacid into a terrestrial canid we need only look at some of the terrestrial viverrids. There is also abundant fossil evidence from America to give a good picture of the broadest features of canid evolution. On the basis of its teeth MacIntyre (1966) identifies *Miacis* as ancestral to the canids. The skeletal proportions of the Oligocene *Pseudocynodictis* already suggest a longer-legged animal than the civet, but one that still retained well spread digits and curved claws (modern canids have a very compact foot with pollex and hallux reduced). *Cynodesmus* from the North American Miocene is an example of the modern dogs' lineage. The African continent, however, seems to have been dominated by a different branch of canids, the Amphicyoninae during the Miocene, and the ancestors of modern genera are unlikely to have derived from these so-called bear-dogs. Savage (in press) has suggested that the ancestors of the living canids might have reached Africa in the Pliocene but he remarks that the immediate ancestries of *Lycaon* and *Otocyon* are unknown and their relationship with *Canis* and other canids are not clear.*

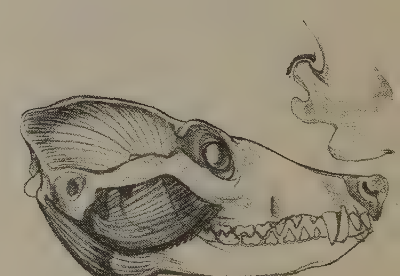
Unlike the cats, this family is not distinguished by a single dental structure or mechanism and the East African genera represent three rather distinct adaptations. The versatile and omnivorous jackals are most typical in having long sharp canines and both cutting and crushing cheek teeth. *Lycaon*, a social courser adapted to kill relatively large animals with lacerating bites and then bolt the meat without bones, has sharp cutting teeth. *Otocyon*, the bat-eared fox, has augmented the number of its teeth in an extraordinary secondary development which can be correlated with an insectivorous diet and a very fast champing action of the jaws. The manner in which teeth increase their number is still incompletely understood. The alignment of jaw muscles in the three genera is completely different and this has been described in some detail by Gaspard (1964). The skull of *Otocyon* is also distinctive because the temporal muscles are short and attached to bony ridges which are separate instead of united in a single sagittal crest, as in most adult carnivores.

Expression is important for all members of this family and they have an elaborate repertoire of ear, mouth and tail movements as well as exaggerated



Lycaon

Canis



Otocyon

Jaw musculature in three canids. Shortened attachments in *Otocyon* are an adaptation for rapid champing of the jaws

Muscle length ratios

	Masseter	Temporalis	Digastric
Otocyon	1	0·55	0·83
Canis	1	0·9	1·33

**Lycaon* is probably closest to the Asiatic hunting dog, *Cuon* while *Otocyon* may be related to the Tanuki, *Nyctereutes*.

postures. The coat colouring of each genus seems to serve rather different functions. The dark extremities of *Otocyon* are likely to be specifically attractive features in the communication system (see p. 55). Emphasis in the blackbacked jackal is on the sides and back of the animal (p. 13). The golden jackal matches the grasses and sands of its open habitat. Living in more humid environments, the darker, grey *C. adustus* is also cryptically coloured. The variably blotched coat of *Lycaon* is discussed in the profile of that species.

All canids have well-developed senses but, according to the genus, sight, scent and hearing are given different emphasis and are significant both in the finding of food and in intraspecific communication.

Social life centres on one or more families living within a hunting range or territory. In jackals, the pair bond weakens periodically but both parents rear the young. The small groups of families that constitute a pack of hunting dogs are, like all canids, ordered in dominance hierarchies. Kuhme (1965a) stressed that aggression, virtually absent or suppressed while hunting and feeding, found expression in males competing for mates and in the competition between females for puppies.

Van Lawick (1974) witnessed a dominant female kill all but one of the pups of an inferior female and then appropriate the survivor and he also saw individual dominance between two females reversed after a fierce fight. The exceptionally large litters and high mortality rate of this species may be adapted to the disruptive effect of female competition as well as to the hazards of canine distemper, babeesia and other diseases to which most canids are susceptible.

Regurgitation, which is a technique employed by many canids to bring back food to the young, has been ritualized and integrated into the social structure of *Lycaon*. The end of a hunt taking place at an unpredictable distance from the young and the den, regurgitation is a canid solution to the problem of transporting food without unbalancing their functionally slender proportions.

All young canids are readily compared with domestic puppies and Van Lawick has perceptively evoked their appeal in his descriptions and photographs.

Lycaon

Jackals and Dogs (Canis)

Species

Canis adustus
Canis aureus
Canis mesomelas

Nobody watching a jackal can fail to be reminded of dogs. Almost every quirk of behaviour, every gesture is familiar and a study of jackals suggests how many of the disjointed mannerisms of their domesticated relatives have been derived from functional patterns of behaviour common to all members of the genus *Canis*.

Since relations between canines (including those between a mated pair and between members of a family) are governed by dominance and submission the communication of an animal's status and intentions is of prime importance. The animals receive unambiguous messages from one another's voice, smell and posture. Growls or whines, the scent of each other's urine or anal secretions, the erection or depression of tail and crest, the movements of lips and ears are information codes carrying much the same messages for dogs and jackals.

Some of the differences between species raise interesting questions. For instance where an angry dog bristles its hackles, the blackbacked jackal, *Canis mesomelas*, has a very precisely demarcated area of specially coloured black and silver guardhairs and a broad black line along the side of the body, indicating that there has been selection for enhanced conspicuousness in this area. In addition to raising their dorsal hair when aggressive, most canines have the habit of asserting dominance by bumping their rump into the opponent. This involves a swing of the body while maintaining an intense face to face confrontation. In the case of the blackbacked jackal this behaviour might be more highly ritualized and might have come to play a more important role in social interactions (see p. 33). Harmless but intimidating, this form of threat can also be implied by a mere sideways turn of the body and the action can be conspicuous if it flashes a visual signal. Such sudden twists can be observed in excited *C. mesomelas*. It is conceivable, therefore, that the bold colouring of their capes and sides flags this peculiar implication of dominance. In some of the areas where the three jackals overlap in range (and *C. mesomelas* has no part of its range entirely to itself) recent studies have shown that the local jackals have differing voices (see pp. 28 and 32). These observations suggest that there is selection for those details of behaviour that help to keep the species distinct. This could explain the strikingly different colour pattern in *C. mesomelas* as a response to widespread sympatry with related jackals. It could be the product of no more than a slight shift in emphasis or frequency within a repertoire of dominance behaviour that is common to all canines.

Of course the jackals occupy quite distinct ecological niches but the interacting patterns of vegetation types in East Africa ensure that there are exten-

sive areas of overlap in this region. I have seen all three species within sight of one another in Laikipia. Here the rolling country has flat well-drained hill tops which are open, grassy and a favourite haunt of the golden jackals. The many water courses which dissect the plateau have dense undergrowth and it is here that the sidestriped jackals live. In between the two are extensive areas of light acacia scrub and woodland where there are blackbacked jackals. There is no recorded instance of hybridization between wild jackals but it has been achieved in captivity. Golden jackal-dog hybrids are known.

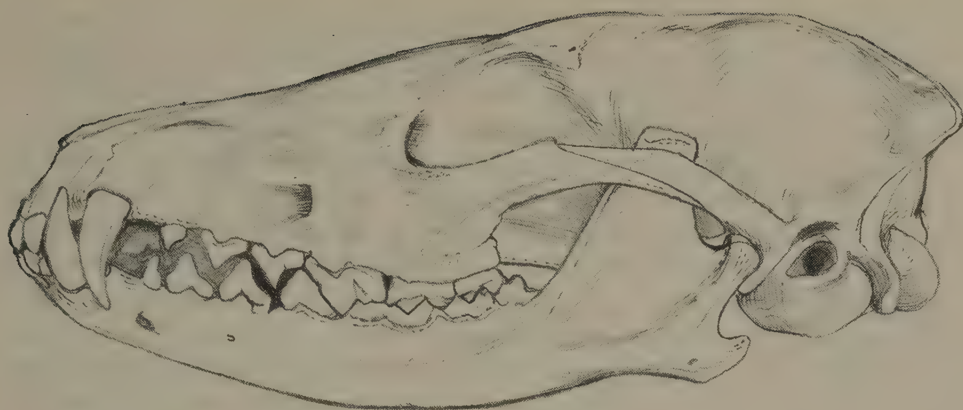
Tropical jackals are unlikely to have been the ancestors of dogs. It is equally unlikely that the first animals to be domesticated were big northern wolves. Domestication probably began in the Middle East or Mediterranean areas and perhaps during the Palaeolithic. Although there are four extinct species of *Canis* in the African Pleistocene alone, the choice of the dogs' ancestors lies between a southern race of wolf and the golden jackal.

Recent studies have shown that jackal families often co-ordinate their movements when they hunt together. Jackals are also very quick to interact with any other species if they learn there is food in the offing, and their behaviour in such situations is sometimes of advantage to a larger predator. It is a very much more likely proposition that an animal with a symbiotic relationship with our hunting ancestors gradually became more and more familiar and useful, rather than that primitive man should quixotically rear the whelps of a dangerous and self-sufficient competitor like the Holarctic wolf, which even when tame does not relinquish or share its food.

When the genus *Canis* is viewed in a global perspective and in the light of new studies, the traditional distinctions between wolves as social hunters and jackals as solitary scavengers have to be qualified. We know that local ecological conditions modify hunting strategies and social behaviour and that the size and abundance of prey and predators are interrelated. Also it must be remembered that although their respective ancestries may be ancient, intermediate forms of *Canis* do exist. For example, the Syrian wolf was much smaller and much more solitary than its northern relatives. The tropical *C. adustus* is, in spite of its size and single-family social structure, more wolf-like than the other two African species. *C. mesomelas* and *C. aureus* are very alike morphologically. Yet the fossil ancestry of *C. mesomelas* is recognized in the Lower Pleistocene, which makes it one of the earliest members of the genus known.

It has been suggested that cave-paintings showing men surrounded by the silhouette of dog-like animals actually represent the use of canids for hunting. Today we use dogs for tracking and bringing larger animals to bay, for flushing, catching and retrieving small game birds as well as for controlling the movements of large flocks of herbivores. These functions might have been equally useful to our hunting ancestors but what is especially significant is that the behaviour patterns on which these services depend can be seen in wild jackals.

The epithet of scavenger only partially describes an important characteristic of jackals. They are quick to discover all sources of food, from large predators' kills, village rubbish dumps and insects around streetlights to highway casualties. They are, in fact, much better described as opportunists and their unspecialized habits can be seen as an adaptation to a diverse diet.



Canis adustus

Trotting round their large home ranges, they are soon familiar with the various sources of food available through constant exploration, and are alert to any repetition of opportunities. Large animals and birds are as much a part of the jackals' surroundings as bushes and termitaries. The last, like the rest of the environment, can be explored for lurking rodents or insects but the herbivores are normally inaccessible to the jackals as food because of their size, agility or dangerousness and are, therefore, ignored. However, whenever a larger animal dies, is killed, produces an afterbirth or a helpless calf, there is an abundance of meat or scraps for the jackals; likewise, when a bird is flightless or can be caught unawares, a formerly neutral feature of the landscape suddenly provides a meal.

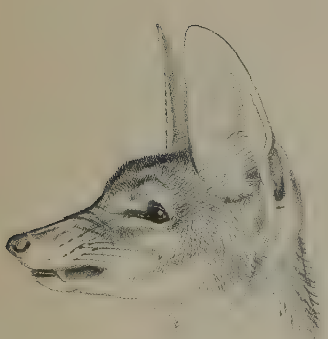
The circumstances in which large animals provide food for jackals are very variable and the jackals' behaviour is appropriately adaptable. For example, a mother antelope's defence of her fawn is generally effective against one jackal but not against two because while one is being chased off the other can kill (Wyman, 1967). The differing roles of killer and distractor are reversible and provide another benefit for the pair-bond, but the effectiveness of hunting as a team is exploited and perhaps improved through experience. Likewise a family of jackals commonly forages along an extended front and individuals often catch the hare or rodent put up by a neighbour. Their attendance on lions or hyaenas is probably learnt in the first place, the jackals coming to recognize the signs of a hunt or a kill and responding in advance to the chance of a future meal.

Jackals do, of course, chase and kill appropriately sized animals on their own but it may be mobbing behaviour that induced our ancestors to cultivate a relationship with these animals. Many dog owners are irritated by their pets' proclivity for chasing and barking at domestic stock and birds. The activity often seems aimless and playful and is generally followed by a tail wagging greeting on return. Very similar behaviour has been seen in wild jackals and they commonly harass large or dangerous animals.

The outcome of such harassment is less predictable than similar behaviour by wild dogs, *Lycaon*, and hyaenas, which rush herds of antelopes and then watch the running animals attentively before pursuing a particular antelope (which is often slow or lame). Indeed, it may be precisely because the domestic dogs' and jackals' chasing is playful that it can serve as an exploratory mechanism. In this way the jackal might realise a variety of potentials for food from sources that might otherwise be ignored. Blackbacked jackals commonly harass young baboons in such a playful manner that the baboons ignore them, yet a jackal was seen on one occasion to disappear down a hole with a young baboon in its jaws before there was any chance of a defensive reaction by troop members. In the course of watching a family of cheetahs, Eaton (1969b) saw the mother get within charging range and kill a gazelle which was distracted by the antics of a jackal which had suddenly run barking into the midst of its herd. Subsequently this jackal and its own family scavenged the remains of the cheetah's kill. This behaviour was seen several times and Eaton considered that the jackal had learned the effectiveness of this technique as an individual. Some months previously it had merely scavenged the cheetah's kills. Other examples of jackals attempting to make a kill after a companion had indulged in the peculiarly ostentatious behaviour of mobbing and of participation in the hunts of other carnivores are described on pp. 20 and 26.

Temporary re-enactment of a pre-dog era was witnessed in East Africa at about the turn of this century when large areas were virtually without domestic dogs following severe distemper and rinderpest epidemics. Percival (1928) remarked on how tame and numerous jackals were around the Masai manyattas at this time. A familiarity that can still be seen occasionally when, for any reason, dogs are absent and the jackals can find abundant food without being chased off.

Like dogs, jackals bury surplus food but return to it within a day. Their retrieval, like their hunting, probably involves both sight and scent. The most intensive hunting activity usually begins before dusk and Budgett (1933) has shown that evening temperatures are ideal for scent tracking. At this time jackals can be seen trotting along with frequent stops to examine and sniff or to listen. The blackbacked jackal has particularly large and mobile ears.



Canis mesomelas

Scent clearly conditions social encounters and anal sniffing is as common as in dogs. Donovan (1969) has found that dogs actively avoid the anal secretions of a dog that has been alarmed and are excited by those of a bitch on heat. Anal scent presumably also confirms an animal's status and sexual condition and occasional deposits of dung as well as urine on grass tufts suggests that both might serve as territorial markers.

Vocal communication is well developed and all three jackals howl, although there are regional differences in this respect (see p. 32). On the one hand howling is a contact device between individuals and on the other hand it has been reported to be largely restricted to the territorial area, wherein an entire family sometimes joins in unison. This ritualized howling might also function as a territorial advertisement but it is stimulated not by neighbours but by the sight and sound of the rest of the family within the security of the home area. In such circumstances the prolonged howling appears to resemble the hooting sessions of chimpanzees (Vol. I, p. 37) and presumably functions to cement family bonds.

A fleet figure trotting the pathways at nightfall, attentive at the abattoir, a jackal is a natural symbol for the mysteries of death. In Ancient Egypt, the jackal-headed god Anubis guided the dead to the judges who would weigh their souls and he presided over the important ritual of embalment. In Ancient Greece, Anubis was identified with Hermes, while Cerberus, watchdog of the underworld might also have derived from a symbolic jackal. In Africa today the jackal features in innumerable stories and is still the subject of multifarious myths.

Canis aureus

Golden Jackal, Common Jackal (Canis aureus)

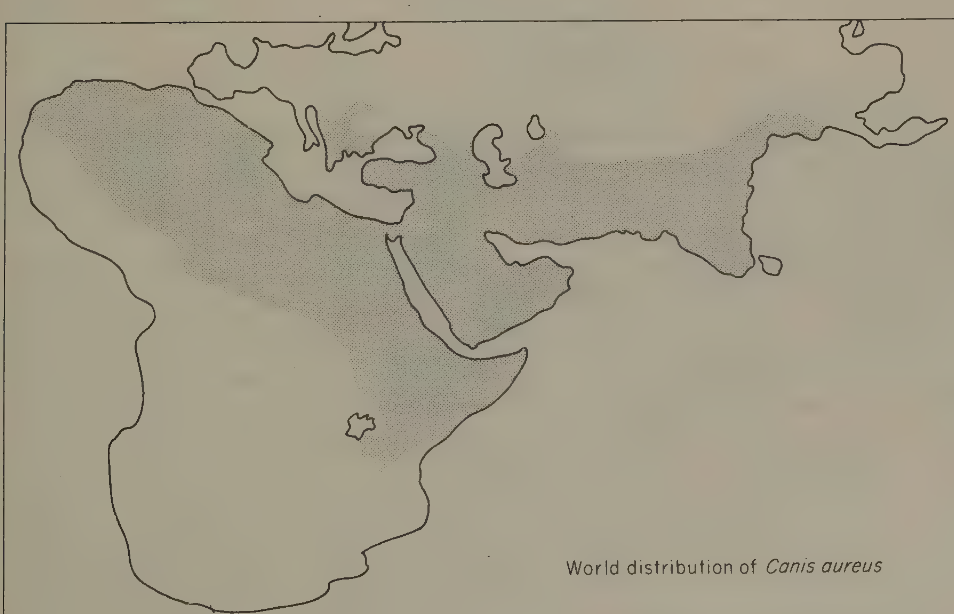
Family Canidae
Order Carnivora
Local names
Bweha wa mbuga (Kiswahili).

Measurements
head and body
74—106 cm
height
38—50 cm
tail
20—30 cm
weight
7—15 kg

Golden Jackal, Common Jackal (Canis aureus)

This species is most readily identified by its sandy colouring and black tail tip. The back has streaks of black and white hair, irregularly scattered through the fawn body colour. Occasional melanistic individuals have been reported.

This species has a very wide distribution in Eurasia and North Africa, where it is mostly found in relatively dry open country, including the Arabian and Sahara deserts. In India, it ranges through a wide variety of habitats but in East Africa it is very restricted, being confined to the driest most open plains and grasslands. The flourishing population on the Serengeti plains is on the south-western boundary of the species' range and there are few other localities in East Africa where they are as abundant. Their pre-eminence on the Serengeti short-grass plains is probably due in the first place to their ability to go without water. They are also well adapted to live off the rather limited food resources available on the plains, subsisting above all on insects, mainly dung beetles and their larvae, grasshoppers and crickets. Wyman (1967) found marked seasonal variations in diet which were not only due to the availability or abundance of foods. A very interesting change concerns gazelles, *G. thomsoni*; the fawns of this antelope are most abundant in January—February and again in July, but Wyman found that while gazelles constituted half their diet during the first four months of the year they only accounted for 27% during the rest of the year. This difference is influenced by the tighter bonds existing between jackal pairs during mating



World distribution of *Canis aureus*

Canis aureus

and whelping, which occur in the first half of the year. During the second half of the year each jackal tends to forage on its own and Wyman estimated a 16% chance of success when one attempted to catch a gazelle, whereas when two or more jackals attacked the rate of success rose to 67%.

Eisenberg and Lockhart (1972) described incidents in Ceylon which suggested co-operative hunting. They observed one of a group of four part company from the others, which dispersed into a forested area where they remained partially concealed but watched the fourth jackal, which was in the open near a pool. This animal herded a plover towards its companions by zig-zagging back and forth. When one of the concealed jackals broke cover and attempted to seize it, the plover flew up at the last moment, whereupon all the jackals came together with wagging tails and touched noses. This procedure was seen more than once. On another occasion a fawn that was being chased by one jackal was intercepted by a second that had been waiting nearby.

The golden jackal tends to keep to the peripheries of a lion or hyaena kill and Lamprecht (personal communication) saw blackbacked jackals chase them away from kills and concluded that inferiority in such competition between jackals might explain why only 3—6% of their food was scavenged. Wyman, however, stressed competition from hyaenas as the main deterrent to scavenging.

Turner (1967) saw a hyaena chase a golden jackal through herds of gazelles and kill it, Kruuk (1972b) saw four hyaenas eating a golden jackal and I have seen one fleeing at the direct approach of a hyaena. Notwithstanding this, golden jackals do sometimes share kills with hyaenas and blackbacked jackals and Van Lawick (1970) photographed a male tugging at a piece of meat with a hyaena. He also thought that they only scavenge when an animal dies or when a large predator happens to kill within their home range, which may be relatively infrequent. Exceptionally conscious of birds in the sky, they can be alerted to the presence of carrion by vultures. The rest of their feeding is very opportunistic; rodents such as gerbils and spring hares, hares, ground birds and their eggs, lizards and snakes, frogs, fishes, bulbs, berries and fallen fruit are all eaten when they are available. In India, the ripe fruits of mango, cashew, fishtail palm and jackfruit as well as melons and cucumbers are favoured foods and even maize may be eaten occasionally.

During the gnu's very short calving season, the Serengeti jackals feed almost exclusively on the afterbirths, guided to newly delivered cows by smell or by the sight of plummeting vultures.

When they kill a medium-sized animal, they tend to grab at it anywhere but soon turn their attention to its abdomen, snapping and tearing without attempting to secure a deadlock.

Seitz (1959) reported behaviour similar to that of other carnivores, released by dead prey and certain unfamiliar kinds of meat. The jackal rubs the sides of its neck against the food and rolls on its back.

The commonest scent marking is by urination. Both sexes were seen by Lamprecht to urinate against tussocks (often the same one) and he saw this behaviour throughout the year, although the incidence might increase during courtship. Golani and Mendelsshon (1971) recorded one making a handstand while urinating (a posture commonly adopted by wild dogs).

The vocabulary of this species resembles that of dogs and Seitz (1959) recognized seven different sounds and remarked that subspecies can be distinguished by their different howls. Their barks are more dog-like than those of the other African species. The same holds true for the greeting patterns but the dominance—submission interactions are virtually the same for all three species of jackal.

The activity patterns of golden jackals are modified by the conditions in which they live. They are strictly nocturnal in areas inhabited by man but are partly diurnal on the Serengeti plains, where Lamprecht has conducted regular 24-hour observations on activity cycles.

While a pair and their young comprise the basic social unit, it is common for the young of the previous year to remain with the parents and a new litter of cubs. Lamprecht saw one group of ten in which there were three adult-sized males and three females, two of which were mothers, each with two offspring. No friction could be discerned within the group. Thus it is possible that young may mature and mate while continuing to share the parental range and den. Lamprecht observed that an adult pair with offspring, marked and defended a territory with a diameter of one to three kilometres. The principal means of marking is by urination but Lamprecht noticed that adults defaecated on top of grass tufts or other vegetation, whereas younger animals were not selective in this way. Seitz (1959) also noted that dung and urine are used for marking and may be spread with the familiar canine scratching of the hindlegs. Outside the breeding season, particularly during the driest time of the year, some individuals wander long distances (Lamprecht, personal communication).

Van Lawick recorded a Serengeti pair using four dens and moving five times in twelve weeks in spite of having young cubs. Long-term tenure of a territory is probably relatively stable, although some jackals from the Serengeti plains are thought to move closer to the woodland edge during the dry season (Schaller, 1972b). Schaller saw thirteen golden jackals congregated on a lion kill. In such circumstances one can presume that the kill had been made on relatively neutral ground or such a rich source of food might cause some breakdown of territorial behaviour. Van Lawick saw fierce fights break out amongst fully grown males feeding at a dead zebra and he saw no more than three adults feed together at a time when fourteen jackals were around the carcass. However, contacts between adult jackals are not always hostile.

Seitz (1959) watched the sequence of behaviour by which the male and female became an established pair. After a threatening display by the male and submission by the female there is a tentative nuzzling and exploration of the forequarters and mutual touching of the flanks followed by inspection

of the genital regions. The female then tends to break off with an invitation to play, to which the male responds. The pair then keep close company and start to hunt prey together. Before mating there is a heightened interest in the genital area and the male often symbolically rises on his hindlegs and both animals howl while he rests his paws on the female's back. Seitz also described what he termed the *Brunst Gesicht* or "mating face" of the male, in which the mouth is opened wide while the hair bristles and the eyes close; the male may adopt this somewhat comical expression during courtship and while copulating. Females also grimace but without closing their eyes; Eisenberg and Lockhart (1972) described a submissive young female extending her tongue out of an open mouth after sniffing at her father's urine which had been deposited in between bouts of rolling on the ground.

After a gestation of two months one to five pups are born in a den, which may be an *Orycteropus* earth or an enlarged spring hare burrow. Most births occur in January and February and recorded births cover the period December–April in Serengeti. Van Lawick (1970) recorded an instance of two litters in one year.

The puppies are very dark at birth and their eyes do not open for ten days. The development of the young has been studied in some detail by Seitz (1959) and is similar to that of the dog.

The colouring changes slowly and by the time they are four months old the young have the pale colouring of the parents, a change which coincides with weaning and increasing exposure as they travel from the den.

The young are very vulnerable at this stage and reports of martial eagles taking young jackals are not infrequent. Van Lawick even saw the relatively small bateleur eagle nearly succeed in carrying away a pup. Leopards also prey on them when they approach thicker vegetation. A not uncommon sight is pairs or even single jackals tackling any hyaena that approaches a den where the young are hidden. The parents embarrass the hyaena by repeatedly nipping at its hocks and rump and generally succeed in driving it away.

Females are sexually mature at eleven months but males only acquire adult build and appearance after the age of two years, although they are probably sexually active at one year. Captives have lived for sixteen years.

Sidestriped Jackal (Canis adustus)

Family Canidae
Order Carnivora
Local names
Bweha (Kiswahili), Akabowa, Ekihe (Luganda), Eboha (Runyoro), Emuha (Runyankole), Too (Lwo), O loo (Karamojong), Bleyit (Sebei), Habila (Kinyiha), Uba (Madi), Bowa (Lugbara), Akambwe, Imbira (Kinyakyusa), Ngewe (Kikinga).

Measurements
head and body
65—81 cm
height
41—50 cm
tail
30—41 cm
weight
6·5—14 kg

Sidestriped Jackal (Canis adustus)

Canis adustus

The sidestriped jackal is drabber in colour, shorter legged and shorter eared than the other species but is more heavily built and it can generally be distinguished by a white tip to the tail and by rather indistinct black and white stripes along the side.

This is the most widespread species in all moister habitats, ranging through various savannas and thicket types to the edges and glades of true forest. It is common in cultivated areas and is frequently seen run over on highways. It is also common at high altitudes—up to 2,700 metres—where it may be more thickly coated and will live in all sorts of mountainous and rough country. It also occupies swampy areas.

This species is more completely an omnivorous scavenger than the other jackals. Judging from stomachs examined in southern Uganda, they feed mainly on insects, fruit and village offal, often bulked down with some green grass. One animal collected on a causeway through a papyrus swamp had been eating the white nymphs of *Dorylus* ants. About one and a half kilos of these, with many adults, were in the stomach while many hundred soldiers were attached to its lips, gums, fur and feet. The animal seemed quite unconcerned about bites and the presence of some *Dorylus* in another stomach suggest that ants may be a common food. I have frequently watched individuals catching winged termites as they emerged from the nest or flew around under street lights in Kampala. The occasional swarms of grasshoppers are also attracted to street lights, and these too are relished by suburban jackals. A captive free-ranging jackal would bump his body against vegetation in order to dislodge the grasshoppers and then would pounce on them when they flew. He dug up earthworms, millipedes and crickets but avoided all types of caterpillars. He would attempt to catch small birds with a short very fast dash. Snakes, *Typhlops*, were killed with fast champing snaps. Food was always taken to cover and seldom eaten on the spot where it was found or given. All sorts of fallen fruit attract jackals and they are known to eat maize while it is still soft and growing on the stem. They catch various insects, mice, small birds by a quick pounce or dash but have never been recorded as running anything down, although they may accompany other predators. I once heard of one of this species visiting a poultry yard where it ate duck mash without attempting to harm the birds themselves. However, Percival (1928) indicted this species for taking the eggs and young of ostriches. In the Ruwenzori park, where this species suffers no competition from other jackals, it lives on the open grasslands around Ishasha and includes the afterbirths of topi in its diet.

Though they normally forage on their own, in pairs or mother-and-young groups, it is possible that concentrated food supplies such as dead ungulates or town refuse heaps may encourage larger groupings. Diet evidently varies from area to area and Bothma (1965) examined three stomachs in South Africa; one contained only grass, one had grass, a grasshopper and a young sheep and the third had fresh oribi meat and hair. There is reason to think

Canis adustus

that the second and third animals had scavenged rather than killed their food as they are not infrequent attendants at kills and often keep up with other carnivores while they hunt.

> "Should you wound a buck and set on dogs to run it down, jackals will frequently join in the chase, when dogs and jackals will take little notice of one another till the quarry is pulled down. Then the jackals stand aside. I saw my dogs tackle a buck and the attendant jackal took no part in the proceeding." (Percival, 1928)

This author also reported that a tame pair were kept with some greyhounds and that they accompanied the dogs in chasing wild jackals of their own species.

Percival regularly hunted this species with a field of mounted hunters and foxhounds and he noted that they generally tried to squat and let the hounds run past or else started by running in rings, behaviour that is typical of a territorial species. Once embarked on a run they could keep it up for 30—40 minutes but if the animal was a female the hounds were sometimes inhibited from attacking it (perhaps she was in oestrus). There are also other reports of dogs which have cornered a jackal suddenly leaving it alone.

When brought to bay, the animal screams but if really cowed or wounded it makes a low croak. I heard this call from a young female which had had her neck broken by a passing car; it had a strong effect on the five jackals attending her, an adult male drawing closest to her, even while she was being examined by people. The most characteristic call of this jackal is reflected in many of the local names; it is an explosive "bwaa", commonly uttered by a single animal while standing in the open at night. Instead of howling, like the golden jackal, this species makes a more owl-like hoot and the onomatopoeic names given by the Karamojong reflect the different voices; *o loo* for *C. adustus*, *kwee* for *C. mesomelas*. Excited yapping is sometimes heard.

Of two captive pups the male was emphatically superior and the two sometimes played with one another, wrestling, mock biting and kicking. A female reared by my son was a passionate participant in his marble and football games, seizing a marble in her jaws but dropping it as soon as she was caught. She would tug at his trousers or nip his legs in invitation to have chasing games and rushed whimpering to him if ever she got kicked or hurt. While running, the tail flounced and thrashed over her back and for some time after any excitement the long hair on the tail was fluffed out.

Although I have seen this species trotting through uninhabited *Brachystegia* woodland during the middle of the morning and on the Ishasha plains in the afternoon, it is generally strictly nocturnal in cultivated areas; perhaps the white tail tip could be regarded as a badge of its nocturnal status. The largest party I have seen was of six animals, of which two were slightly bulkier than the others, suggesting a pair with four near adult offspring. As many as eight or twelve have been seen at kills or in townships, but it seems likely that the family is the normal social unit. Judging from observations along roads in southern Uganda (where it is very common) pairs are well spaced out. The tendency to run in a circle when hunted has been mentioned and its sedentary habits have been attested to by numerous observers. Percival

(1928) reported that the same earth is used year after year and I was brought two puppies from a den inside an old termitary which had apparently housed several litters over the years. Termitaries, *Orycteropus* holes, and burrows in hillsides appear to be favourite sites for whelping, although older pups and adults quite often lie up during the day in thick vegetation.

I estimated the births of four Buganda litters as June—July and September and Percival thought there were more young about in southern Kenya during September and October than at other times. Ansell (1960b) lists a Zambian birth record for June and noted young between September and November. Litters range between three and six. Wolhuter's record of a pregnant bitch with twelve foetuses suggests that there may sometimes be some resorption of foetuses or other early reduction in the numbers of the litter. Gestation periods have been variously listed as between 57 and 70 days. Growth is fairly rapid and quite young animals can sometimes be seen foraging on their own.

They are alert and quick and the young are capable of hiding in quite insignificant patches of vegetation, as my son's captive frequently demonstrated whenever she was due to be returned to her run.

In spite of their powerful scent the puppies are sometimes domesticated, becoming the equivalent of one-man dogs. A cross between a jackal bitch and a fox terrier was apparently more like the father. A most extraordinary case of fostering occurred in the West Nile area of Uganda. One night in September 1953 a female oribi was found lying down with what appeared to be young ones. When the oribi stood up and started to move off it was discovered that the young animals were five jackal cubs. The cubs were definitely accompanying the female oribi which appeared to encourage the relationship (U.G.R., 1954). It is interesting that this incident occurred at a time when the West Nile district was the source of an outbreak of rabies and large numbers of these jackals were being trapped and poisoned.

Jackals suffer from distemper and Percival reported them dying in thousands during the Kenya epidemics of 1906—7. *Babesia canis* from healthy *C. adustus* have been found to cause symptoms of the so-called tick-fever in dogs. Jackals might therefore represent a reservoir for this canine disease.

Jackals are the subject of much superstition. In some areas their howling is thought to be an augury of death nearby and their skins and nails are sold

in Kampala and other markets as fetish components to ward off evil spirits. The heart is boiled in parts of Buganda, where it is believed to cure epilepsy. The most important Kiganda belief concerns "Kutamukago" a blood relationship with the jackal which binds the participant in friendship to all jackals so that they can never be used as vehicles or disguises for spirits sent to cause harm. Paradoxically, the "Kutamukago" relationship requires the killing of a jackal and in modern days even running it over with a car will serve (K. Sempangi, personal communication).

Blackbacked Jackal (*Canis mesomelas*)

Family Canidae
Order Carnivora
Local names
Bweha Nyukundu (Kiswahili), Gedala (Kiliangulu), Mola (Kinyaturu), Ekwee (Ateso), Nchewe (Kihehe), Ngewe (Kikinga), Kwee (Karamojong), Kewe (Kisagara), Muzozo (Kitaita), Nhyewe (Kigogo).

Measurements
head and body
68—74·5 cm
height
38—48 cm
tail
30—38 cm
weight
8·5 (7—13·5) kg
males average 1 kg more than females

Blackbacked Jackal (Canis mesomelas)

Canis mesomelas

The blackbacked jackal is easily recognized by its slender build, large ears and sharp contrast of the pale, rufous limbs and body with its black back, which is streaked with white. The tail is black-tipped.

This species is essentially an inhabitant of the rather dry communities of Somalia and south-west Africa where its habitat is principally *Acacia* and *Commiphora* woodlands and thickets.

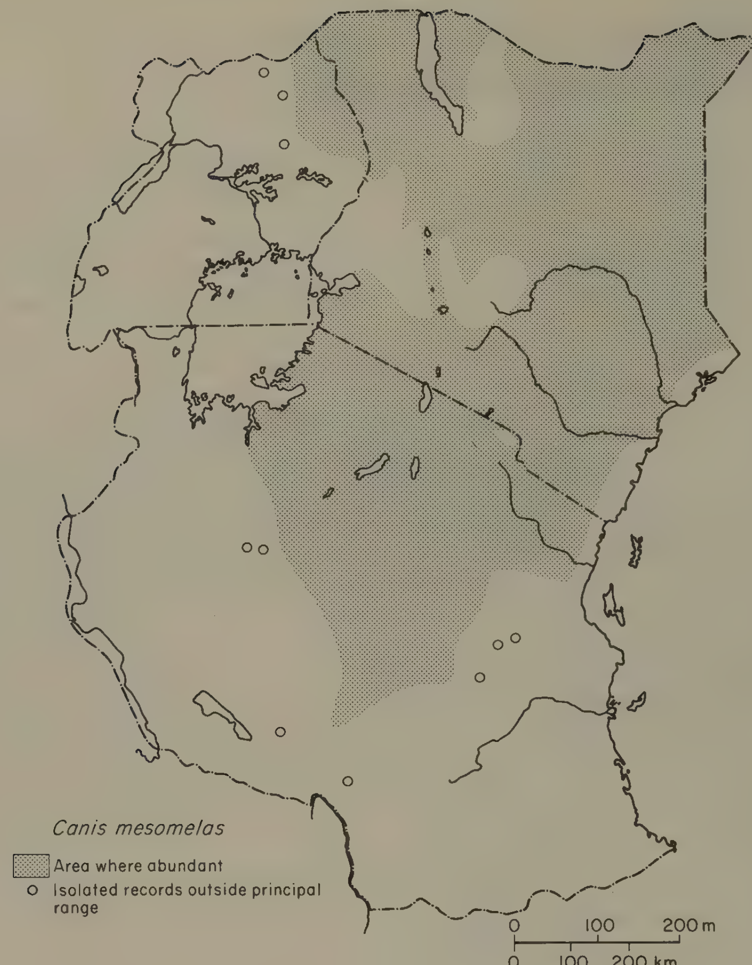
Fossils of this species are known throughout the Pleistocene, so it would appear to be an exceptionally stable and ancient form, though whether any more so than its relations it is not possible to say.

The recorded foods of this jackal are diverse and plant foods are not uncommon, particularly fallen fruits, groundnuts, berries and grass. Beetles, termites, grasshoppers, crickets and winged ants are common; as are spiders, scorpions, crabs, frogs, lizards, various snakes, including several very poisonous species, ground-dwelling birds and their eggs and nestlings, ranging from quails and larks to ostriches. Mammals range from shrews, hedgehogs, various rodents including porcupines, mongooses, young bat-eared foxes, hares and a wide variety of young ungulates, including gnu, kongoni, impala, lesser kudu and cattle. Of adult antelopes, dik-dik and Thomson's gazelles seem to be the upper limit of its killing capacity but it may tackle sick adults of larger species and a pair have been seen harrying a wounded bull rhino which could barely walk.

When attacking they may snap and bite at the legs and loins of a taller animal but very frequently they go for the neck, where a tight hold may be maintained. Carrion is important in areas where there are large herds and numerous wasteful predators such as man and lions or a prevalence of disease, but for the most part they are capable hunters. The rapidity of their movements and their boldness in the face of lions and hyaenas as well as their aggressiveness towards other jackal species and scavenging birds seem to operate to their advantage; for Wyman (1967) noted golden jackals in Ngorongoro eating only 6% carrion in spite of their being three times as common as the blackbacked and, despite the latter species' smaller population in Ngorongoro they invariably outnumber golden jackals at kills.

Serengeti jackals change their diet according to whether they are hunting alone or in pairs. Wyman has reckoned that half their diet consists of insects during the early months of the year while they forage individually but once pairs have formed insects become relatively unimportant and the predation rate on gazelles rises significantly as their effectiveness at hunting them increases. Although a jackal may glut itself on a fresh kill, particularly if it has to carry some back to regurgitate to its young, it will usually hide surplus food in a scattering of caches to which it returns within twenty-four hours; a mean daily consumption of one kilo has been estimated.

The close association of this species with larger predators has been mentioned; in South-west Africa, Shortridge (1934) described them joining up with brown hyaenas to scavenge the sea-shore in parties and it is not uncommon for them to follow lions in East Africa, sometimes yapping as



they do so. This noise is always associated with a disturbance and Lamprecht (personal communication) regards it as a mobbing call which has nothing to do with food.

Neither Kruuk nor Lamprecht heard blackbacked jackals howl in Serengeti, whereas the golden jackals do so very commonly. The head is thrown back with the same gesture as in howling but they yap instead. Further south howling is interspersed with yapping and in the Kalahari Kruuk found blackbacked jackals howling just like the Serengeti golden jackals, which suggests that in areas where the species overlap there has been selection to reduce the ambiguity of each species' vocal communication.

A single yap seems to assist contact between members of the family. Fighting is accompanied by much cackling. Otherwise very dog-like whines and woofs signify want and warning respectively.

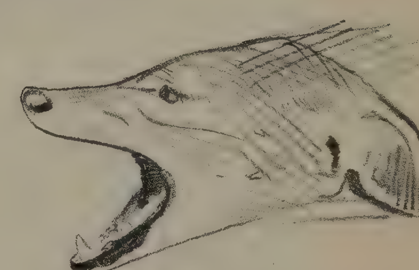
Hunting as they often do in long grass, blackbacked jackals use their big ears a great deal and have frequently been seen pouncing on rodents or quails, evidently guided by sound.

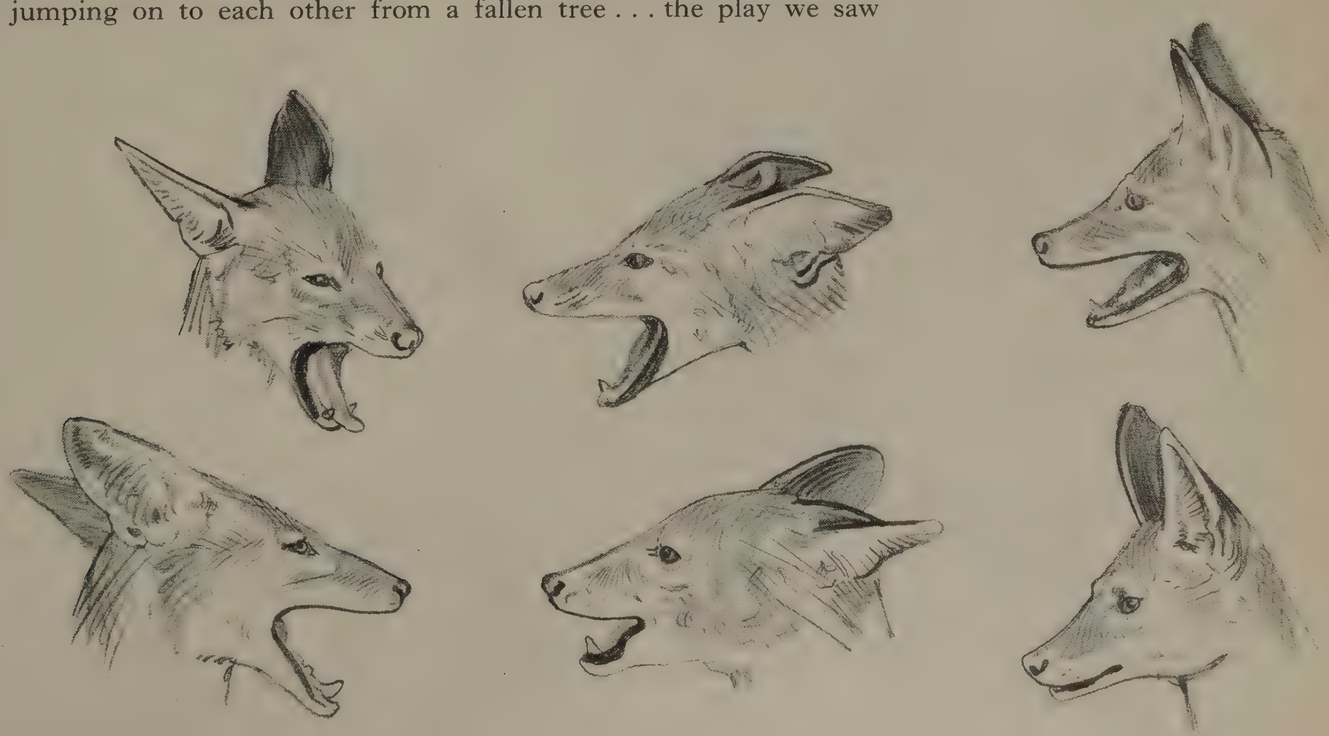
They are primarily crepuscular but their activity patterns are probably adaptable to conditions. They are certainly entirely nocturnal in well-settled areas. In some of the national parks they are much more in evidence

during the day, particularly during the wet season, and disturbance or persecution from humans and dogs probably accounts for the difference.

As in the other jackal species, the family is the basic social unit (Van der Merwe, 1954) but it does seem that social behaviour is more highly developed and that these jackals are sometimes more mobile than the other species. Lamprecht (personal communication) found territories to be of similar size to those of the golden jackal; they are marked with urine and defended. Young of the previous year are often tolerated in the territory of a pair with pups. They often rest near the den and join in harassing any approaching hyaena. They play with the cubs and groom them but Lamprecht never saw them actually feed the young in Serengeti. In South Africa, Van der Merwe (1954) described young blackbacked jackals dispersing as a result of parental intolerance.

Remembering how the moving of the prey herds on Serengeti encouraged two classes of social organization in lions, Van Lawick (1970) thought there might be a similar division of sedentary and nomadic jackals in the Serengeti plains. Noting unpaired adults and subadults commonly in groups of six or more and the frequency of playful interactions, he photographed and described a typical incident between two such nomads. As a dominant animal approached, the other male raised its front paw high in the air and, when the other stopped, touched him on the shoulder as if warding him off, a gesture commonly seen in foxes and wolves (Fox, 1971). The dominant male responded with a swing of his rump which crashed into the other's body. This body slam was repeated twice in quick succession, ending with a backward kick. The dominant jackal then trotted off, only to reappear with a piece of dry dung in his mouth which he laid on the ground in front of the other male. When the subordinate jackal made no move, the other again picked it up and tossed it high in the air with his mouth, hitting it forward with its nose as it fell. "Once more he threw it up and this time caught it as it fell. Now at last the subordinate male got up and for the next half hour we watched as they played, chasing round and round a bush, tugging at opposite ends of twigs, jumping on to each other from a fallen tree . . . the play we saw





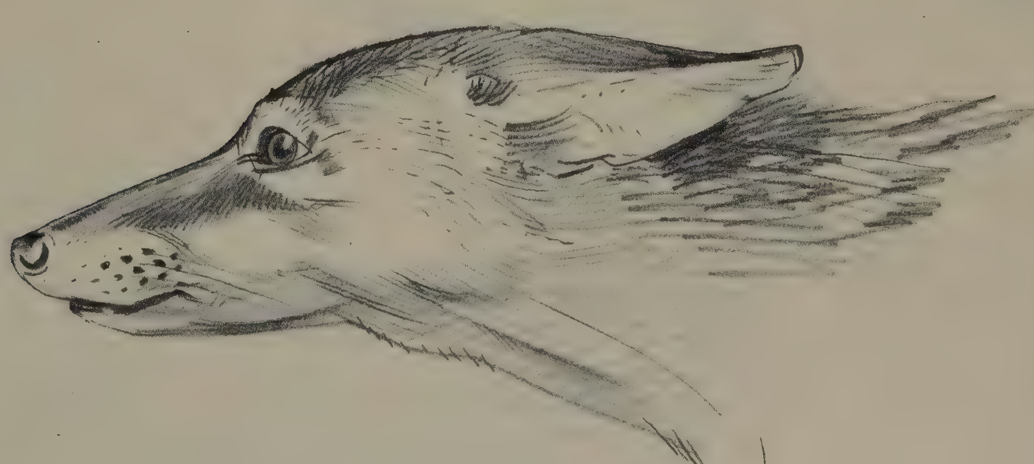
between the nomadic silverbacks sometimes involved as many as six fully mature jackals and lasted up to half an hour." (Van Lawick, 1970). Dominant wolves also seize a bone or some other token food and parade with it growling. This induces symbolic begging from all the other wolves which cluster round him. On dropping the token the others converge in a rush but then ignore it. Schenkel (1967) saw this in the early mornings at Whipsnade Zoo and interpreted it as a ceremony of social integration having the effect of reducing social distance. Similar considerations may apply to the blackbacked jackal and such behaviour might allow the establishment of temporary hierarchies and larger social groupings than the family. These could be advantageous for co-operative hunting among the nomadic class and for effective sharing of large dead animals.

Wyman (1967) estimated a 50% increase in hunting effectiveness when more than one jackal hunted gazelles. In South-West Africa, Wilhelm (1933) noted ten or more jackals assembling to hunt together through a district during the dry season and as many as 20 or 30 have occasionally been seen together on lion kills (Astley Maberly, 1963).

Their sexual behaviour is indistinguishable from that of the other jackals, as is their two-month gestation. In Kenya, Uganda and northern Tanzania most young are born between July and October. As many as nine young have been recorded but four is a more usual number. Their development is similar to that of other *Canis* species.

The den is very often an excavated termitary or aardvark hole. Dens are moved from time to time, especially after a disturbance. Facing dangers from various eagles, this species is also a favourite prey of the leopard.

Captives have lived up to fourteen years.



African Wild Dog, Cape Hunting Dog (Lycaon pictus)

Family Canidae
Order Carnivora
Local names
Mbwa mwitu (Kiswahili), Kikwau (Kitaita), Mbawa (Kikuyu, Kimeru), Imbwa (Kimaragoli), Mulula (Kinyiramba), Kite kya negereni (Kichagga), Mauzi (Kizigua), Eminze (Kibungu), Nzui (Kikamba), Mhuge (Kisukuma), Mbughi (Kinyaturu), Inpumpi (Kinyiha), Ligwami (Kihehe), Liduma (Kibena), Omusege (Kijita), Muthige (Kikuyu), Sudhe, Orude (Lwo), Apeete (Ateso), Osuyiani (Masai), Suyo (Kalenjin), Suyian (Samburu), Kulwe, Suyondet (Sebei), Eeyeyi (Kiliangulu).

Measurements
head and body
76—112 cm
height
61—78 cm
tail
30—41 cm
weight
25 (17—36) kg

African Wild Dog, Cape Hunting Dog (Lycaon pictus)

Lycaon pictus

Wild dogs resemble some of the larger more powerful breeds of domestic dogs in build but they have four toes on each foot, the head is surmounted by enormous round ears, they are marked with an individually variable pattern of black, yellow and white blotches and they have a strong musky smell. For hunters that are very social but inclined to get separated on their twice-daily chases after prey, there is a high premium on regaining contact. This is most easily done by keeping pack members in sight, for which the bold pattern and particularly the white-tipped tail (a colouring which is common to all wild dogs) is well adapted for conspicuousness. When the pack has become more dispersed, wild dogs, like hounds, will track one another down and the exceptionally strong scent emitted by their anal glands must scent even the most difficult trail and thus ease the task of reuniting pack members. It should be mentioned, however, that wild dogs never hunt by scent. Like all dogs their ears participate in a repertoire of exaggerated expressions but the large size and the shape are evidently well designed as sound receptors for the peculiar bell-like hoots with which dogs regain contact with one another; the dogs can probably hear this resonant call over greater distances than the three or four kilometres that it is audible to the human ear.

The coat pattern resembles that of some domestic animals in that it varies from individual to individual; yet the muzzle is always black and the tail tip always white, the latter serving as a highly visible flag while the black lips contrast with the white teeth and pink gums and thus emphasize the expressions of the mouth, which together with the movement of the ears and carriage of the head, body and tail constitute the wild dogs' visual communication system.

Petzsch (1955) has discussed the genetics of colour pattern in *Lycaon* and it is clear that there is no selective pressure for crypsis nor for any consistent pattern elements beyond those mentioned above.

The marbled pattern of wild dogs has intrigued many naturalists. An early suggestion was that the coat was camouflage. It does indeed follow the principles of military camouflage but only in the sense of breaking up the body outline and not in the sense of matching the environment. Preying as they do on grazing ungulates they spend much of the year exposed on the open grasslands where their technique of chasing prey does not require them to merge with their surroundings.

Most predators and their prey require to be inconspicuous at certain times but wild dogs have no need for subterfuge since their young are born in a hole (they are protected by the pack or by their own speed when older) and the pack's hunting is not preceded by a stalk but depends on the persistence, speed and stamina the dogs bring to the chase.

Another suggestion has been that the pattern assists individual recognition (Ewer, 1973). Although the markings do allow individuals to be recognized by an observer, marbling is not the best of systems for such a purpose

and there is little in their social behaviour to suggest that individual distinctiveness is at a premium, and isolated individuals may actually become targets for group hostility. Schaller (1972b) has suggested that the pattern helps to keep the scattered pack members in visual contact during the hunt but I think this function is more specifically served by the white-tipped tail. The peculiarity of their pattern is such that it may incidentally serve to distinguish pack members from their prey so that dogs are unlikely to be confused in the heat of the chase or at a kill and so will avoid biting one another.

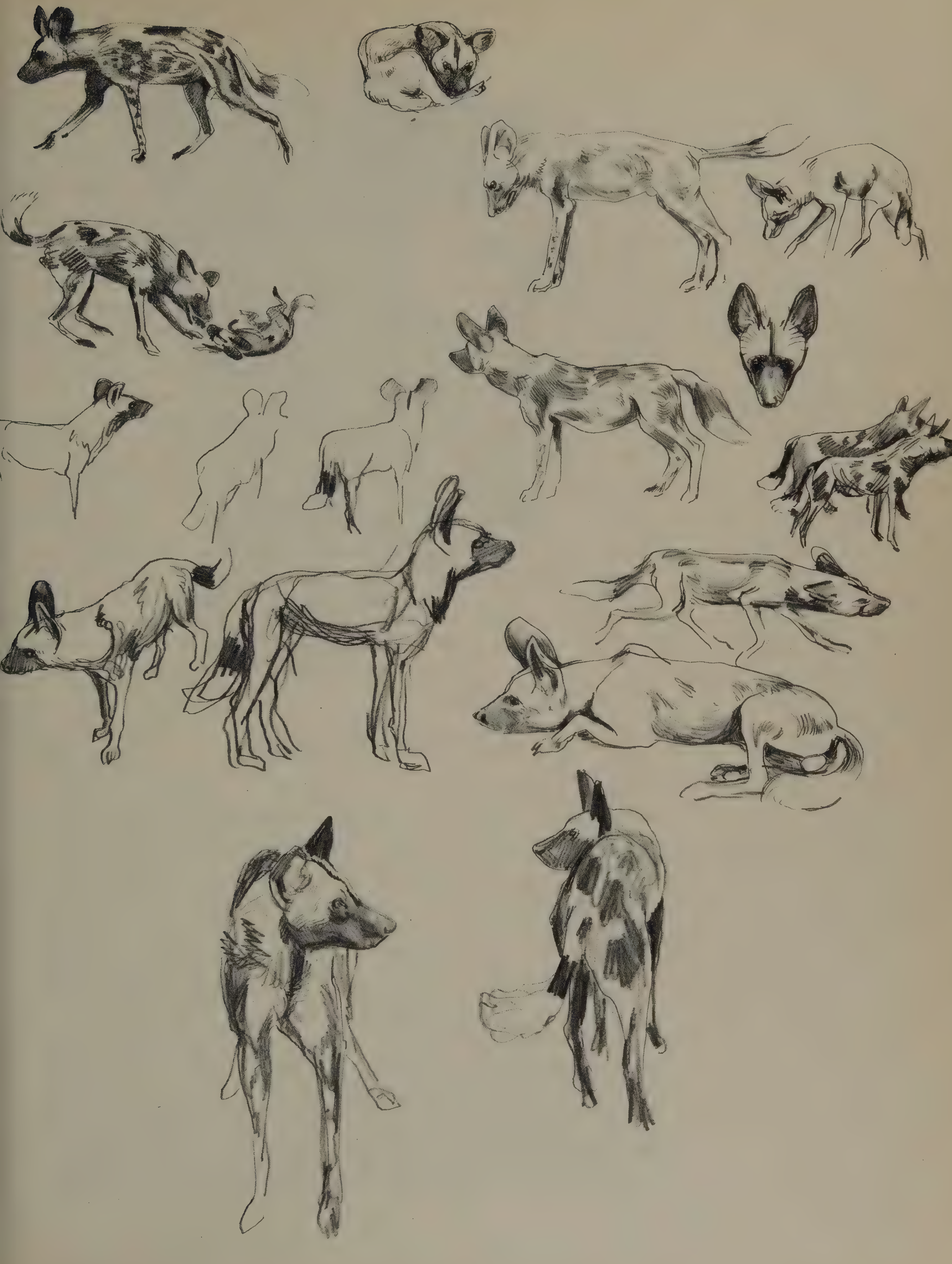
I believe the visual properties of their coat pattern may have a relationship with the underlying disciplines that maintain the cohesion of the pack. Any tendency for young to wander or scatter is a disadvantageous trait in mammals with large litters and a variety of mechanisms control the young and encourage the latter's cohesion. In wild dogs the pups have an inborn tendency to keep very close to one another and bunch tightly in response to any alarm, but this is reinforced by adults carrying wanderers back to their siblings or even threatening them and so provoking the bunching response. As will be shown later (p. 44) the mechanisms for promoting a tightly knit society seem to derive very largely from juvenile traits and from *Lycaon*'s unique feeding behaviour which starts as soon as the young are properly co-ordinated at the age of one month, when weaning on to meat first starts.

The meat is bolted at the kill and then regurgitated for the puppies at the den. As if to suppress anti-social competition and ensure equality of opportunity a gorged hunter's compulsion to regurgitate appears to be strongest when begging comes from the whole litter, whereas a puppy that stands out on its own may be snapped at. Adults also tend to attract group aggression when on their own.

When one considers the visual cues available to the aggressor in its discrimination against individuals, the coat pattern assumes a special interest and their behaviour suggests that there are advantages for the individual to be "camouflaged" not against the background of its habitat but in relation to other members of the pack. Neither the dogs overall silhouettes nor the individuality of the markings are easily distinguished while they are in close formation and the visual impact of a pack is of swirls of black, white and yellow. The strength of their contrast tends to dissolve the body's shape, while the randomness of the markings gives the illusion that each dog merges with its neighbour. This effect is heightened when the pack start the circling, romping movements of their twice daily meet ceremony (see p. 45). It is perhaps significant that optical illusion of anonymity is strongest at a time when aggression is at its height and there is the highest premium on group activity. The importance of maintaining contact is critical because the dogs range over very large areas except for periods when there are young puppies to be cared for.

The extensiveness of their wanderings and their relative rarity make an estimation of their status and total distribution rather difficult, as packs wander in and out of areas where they have not been seen for many years. They have been reported from most of the grasslands, savannas and woodlands of East Africa with the exception of parts of semi-arid northern Kenya.

They are most commonly seen on the open "game plains" of southern Kenya and northern Tanzania. The preference for open country is partly



NOTE This distribution must be seen in the light of *Lycaons* exceptional mobility. Please refer to Vol I pp. 30, 108

real inasmuch as the dogs depend upon the antelope herds which are easier to find and hunt on the plains, and partly apparent in that observers have tended to gravitate to these ideal viewing localities. In the miombo woodlands the dogs tend to follow the herds as they concentrate on the open grassy "mbugas" during the dry season, whereas both dogs and their prey are dispersed during the rains. Prey may be more difficult to find and hunt in hilly wooded country and it is possible that populations of wild dogs live at lower densities in the woodlands than on the plains but the chances of sighting or following these nomadic animals are greatly reduced by the poor visibility and more broken terrain. However, in terms of area most of the wild dogs' East African range comprises the miombo woodlands of Tanzania.

The bold and open approach of a wild dog pack is ill-suited to hunting shy solitary prey, while the need for every member of the pack to have its fill demands consistently successful hunting, which can only be met by preying on gregarious animals of a size that can be easily tired and killed by the dogs. This effectively means that wild dog populations are dependent on an abundance of medium-sized gregarious ungulates such as impala, Thomson's gazelle, gnu, hartebeest, topi and kob, and the areas of East Africa in which

these dogs are most frequently sighted broadly coincide with the distribution of these antelopes. Wild dogs do, of course, hunt a much wider range of species than this and they frequently kill warthog, reedbuck, oribi, duiker, waterbuck, Grant's gazelle, zebra, bushbuck, ostrich and numerous smaller animals including dik-dik, hares, spring hares and cane rats. Of larger animals they have been recorded attacking rhino and one observer drove a pack off a hippopotamus which they were biting in the chest and legs, whereupon they formed a semicircle round two elephants, which raised their trunks, trumpeted and retreated backwards. Ionides (1935) found a pack feeding on the carcass of an elephant he had shot and Kruuk (1972b) also recorded them feeding on carrion although this is unusual, for a pack regularly kills twice a day. Records of the number of chases ending in failure range between 10 and 30%, which is low by comparison with other hunting carnivores.

Their hunting technique varies within fairly narrow limits and consists of a silent approach followed by a fast chase that may clock up to 66 km an hour and averages less than 2 km distance, during which the legs, belly and anus of larger prey are bitten until it comes to a halt, while smaller animals are simply pulled down and torn apart. Wild dogs probably learn by experience how best to hunt particular prey species. For instance, territorial antelopes tend to run in wide circles, which allows the dogs to cut in on them and thus gain continuous advantages. In such circumstances the chase may be relatively leisurely and the prey is soon worn out and outmanoeuvred without much effort on the part of the dogs. Other species such as gnu may be deliberately panicked by a headlong rush in which the dogs are quick to seize upon any animal that has been rendered vulnerable either by its own actions or through some disability.

The fauna of a region, its vegetation cover and topography influence their diet and the procedure of hunting. Where prey is near a safe refuge, the dogs may be more careful and silent in their initial approach and then make a very fast rush. By contrast, dogs have been seen to exploit their prey's dependence on water in the dry season, by remaining close to a waterhole and ambushing them when they come to drink but this is not a characteristic strategy for wild dogs. It is nonetheless an interesting example of their ability to take advantage of a short-lived phenomenon, particularly since the dogs themselves appear to be in less frequent need of water than their prey. Schaller (1972b) noted that individual packs acquire a taste for hunting a particular prey. On the open plains of Serengeti, Thomson's gazelle are most frequently killed and estimates of their relative importance range between 42 and 69% of the prey animals. Gnu follow with between 18—38%. In the bushy Kruger Park, Pienaar (1969) assembled records of 2,745 wild dog kills, 87% of which were impala, 5% kudu and the remainder comprised eighteen species of prey. In the Kafue Valley, Zambia, Mitchell, Shenton and Uys (1965) estimated that bushduiker and reedbuck constituted half their prey in about equal parts, with hartebeest 15% and impala 2%; animals killed by wild dogs in this area included two lions and a porcupine.

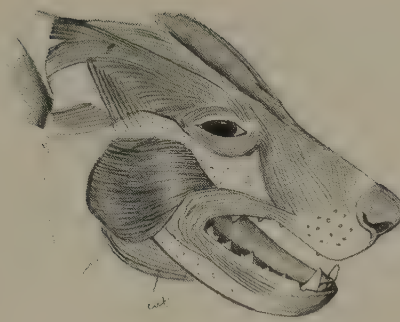
Smaller prey such as rodents, hares and birds are generally caught by individual dogs hunting alone and they are located in long grass by hearing rather than by scent. Sometimes mice are batted at with the paw and snapped at before being eaten but cane rats with their dangerous teeth and the spiny

porcupine must require a well-placed and fast bite for the dog to avoid injury. The dogs have been seen to employ tactics similar to those used by human hunters to catch cane rats; they make noisy leaps down into the grass and, following the rats by ear, drive them along through the grass until they are able to pounce on one.

All prey is eaten very rapidly and smaller animals are eaten up entirely. The larger antelopes are stipped of their meat and viscera; sometimes the head, skin and skeleton are left.

A high proportion of all prey species are juveniles or subadults but this is particularly true for the larger antelopes and there is a correlation between the numbers in a pack and the size of the prey that is tackled. Large animals are much more difficult for a small pack to kill and they may take over half an hour to pull down an adult gnu whereas most prey is dispatched in two to five minutes. Kruuk (1972b) has pointed out that wild dogs consistently hunt smaller prey than spotted hyaenas living in the same locality.

Lycaon has socialized its behaviour and hunting to the point where solitary living and hunting is only resorted to as a very temporary expedient. Lions and hyaenas are much more adaptable in this respect but their social bonds are correspondingly weaker. Nonetheless, it is possible that the size of wild dog packs may be adjustable, with larger units breaking up into smaller ones or very occasionally amalgamating into larger groups. A pack of 40 in the Mikumi Park was observed to split up into three subgroups (the composition of which was unfortunately not noted). In eastern Africa packs commonly number about ten to twelve comprising several adult males and females with some juveniles; larger packs have more young animals of all ages and may number up to 60. Before so much of the fauna was destroyed in South Africa, Gordon Cumming (1850) described packs of several hundreds and Karen Blixen saw a troop of about five hundred in Masailand which cantered past her "looking neither right nor left, as if they had been frightened by something, or as if they were travelling fast, with a fixed purpose on a track. They just swerved a bit as they came nearer to us; all the same they hardly seemed to see us, and went on at the same pace. When they were closest to us, they were fifty yards away. They were running in a long file, two or three or four side by side, it took time before the whole procession had passed us." On the Serengeti, Kruuk (1972b) has recorded that interchange between packs takes place but is relatively rare. However, it has not proved possible yet to keep tracks of the movements and interactions of nomadic packs, except for the three months during which their activity centres around a den with puppies. Consequently, very little is known about what mechanisms underlie the splitting or amalgamation of units and the relationship between neighbouring packs, although Kühme (1965a) has described an encounter in which a peculiar call was heard and much barking after which the two packs retreated back whence they came. Notwithstanding our ignorance of the broader relationships among packs, several observers have studied breeding groups around their dens and recorded interesting details of the development of the young and of social and hunting behaviour. Of many peculiarities in their social life the most striking is the rarity of serious fighting (which would be very dangerous if they used their jaws as they do on prey), and their co-operative hunting and sharing of food. *Lycaon* is



distinguished by special physiological mechanisms that allow food to be shared out and these have provided the dogs with the means of suppressing conflict. Like *Canis*, *Lycaon* employs ritualized appeasement gestures that derive from infantile submission. They whine, cringe, wag their tails and fall over to expose the underside, genitalia and neck, very like domestic dogs, but Kühme (1965a) showed that the suppression of dangerous fighting in this species has been achieved through the ritualization of food-begging gestures which deflect aggressive responses in a variety of different situations. This development has been dependent upon the swallowing and regurgitation technique by which hunting dogs bring food back to the puppies, mothers and any other pack members that remain in a den. Lycaon's ancestors probably gained an initial advantage over competing carnivores and scavengers by eating part of their prey while it was still alive and bolting the remaining meat as fast as possible. The capacious stomach having proved a safer, more economic carrier of food than the jaws, it was a small step to develop the common faculty of throwing up the contents of the stomach in order to feed the young back in the safety of the den.

Observation of contemporary hunting dogs suggests that the hungry importuning by the puppies might have provided the original stimulus for regurgitation but it is also obvious that the regurgitation impulse is now so integrated into the species' life history that a gorged dog often appears to solicit the young to be relieved of the meat. Not only puppies but other adult dogs need only nuzzle the lips to receive a share and I have seen dogs throw up meat when there was no obvious stimulus at all. Perhaps it is the strength of this food-sharing impulse that allows the young to bite and worry a hunter aggressively. The hunter is generally inhibited from making any sort of aggressive response until it has regurgitated.

One result of this behaviour is that the hunting dog's mouth has acquired an attractive connotation (at least for members of its own pack) that is superimposed on the threat that is usually implicit in a display of teeth. For example, one dog's yawn will often draw a neighbour over to put its nose between the open jaws. *Lycaon* does not need an elaborate vocabulary of sounds and grimaces to enforce a hierarchy but facial expressions are less exaggerated than in *Canis* and this may be partly due to the changed significance of the mouth.

In the relationship between feeder and fed the aggression of the latter and its inhibition in the former has allowed *Lycaon* to evolve a paradoxical solution to the problem of containing aggression. Food-begging has not only removed the problem of competition for food, it has provided a system by which the weaker can coerce the stronger without either party resorting to unrestrained biting. Dogs of both sexes and all ages will beg by licking or even biting at the lips and in the case of females at the mammae (which also betrays infantile origins, as even old males attempt a ritual suck). Sometimes a dog will prostrate itself in front of another member of the pack and from this prone position coerce its superior. This tactic may be used to induce regurgitation, to gain access to a prey carcass, or to divert an attack.

Feeders are not always inhibited from attacking beggars and the exception is a significant one. Puppies that rush forward ahead of their siblings are liable to be snapped at. As they tend to bunch up if alarmed, the adults'

threats simply insure that a tendency to compete for an extra advantage is not rewarded and a group approach is assured. This early training in social feeding has relevance for their future as adults hunting in a pack.

In one way or another mouth-to-mouth nuzzlings have several contexts. It is not surprising that the begging gestures with which gorged hunters are met on their return to the den should have become a mode of greeting but they are also incorporated into a ceremony that terminates the night's or afternoon's rest and is associated with the pack's departure for a hunt. This ceremony is distinctive and can be called the meet. Each morning and evening the dogs precede a hunt with a more or less predictable sequence of actions. Individuals emerge from their mud wallows or patches of shade and go over to sniff and lick the mouths of other dogs and younger members of the pack whine or twitter as they search for milk or run from mouth to mouth. Soon all pack members are circulating among their fellows, each greeting being a symbolic solicitation for food. Meat can be regurgitated several hours after a kill, but it is not possible after the afternoon's or night's rest and it is, perhaps, an element of frustration that prompts a visible rise in tension as the meet proceeds. Senior dogs may snap at subordinates and the fear of the latter is betrayed by their urinating and defaecating as they whine like nervous domestic puppies, sometimes falling on their backs in appeasement.

The most important function of the meet seems to be the temporary bonding of dogs and their galvanization into common activity. At its simplest the bonding consists of two dogs keeping up their mutual nuzzling while walking or trotting around seeking others to solicit. A subordinate status may be implied by one partner's tendency to lower its chest and neck below that of the other while synchronized urination is also characteristic of the meet and some males will even handstand in order to superimpose their urine on that of their companion. However, roles are interchangeable and observers have been unable to see any consistent hierarchy during the meet. Pairs may be joined by more dogs and the excited clump may mill around the resting area in circles twittering, pressing all their mouths together and with a bouncy gait, leaning or rocking their shoulders against one another.

A great deal remains to be learnt about the interrelationships between wild dogs but much of the coupling and grouping that takes place during the meet is probably fairly indiscriminate. Particular pairs or subgroupings might tend to stick together as they do during resting periods and traditional or hierarchical associations might influence the contacts that every dog appears to seek. As excitement rises there is much chasing and even the occasional somersault (Van Lawick, 1970). There is also nipping and pawing and if the provoked animal responds both antagonists may rise to their hindlegs and fight. Such fights are normally restrained and ritualized with the emphasis on throwing the opponent off balance by twisting the neck rather than forcing a retreat. Very often the contest ends in the pair running along together still mouthing one another.

The playful nature of the meet has been emphasized by several observers and Schaller (1972b) thought the mobbing looked as if the dogs were trying to induce others to join them by a show of "friendly aggressiveness". This description fits the behaviour very well but variations in degrees of friendliness or aggressiveness reveal that there are several counter-measures (chief

of which is the neutralizing effect of food-begging gestures) that can deprive real aggression of its perils.

Kühme (1965a) has stressed that the meet ceremony is the most intensive of the species' social contacts. He has also pointed out that dogs very frequently approach one another in the same slinking posture with which they threaten a hyaena, vultures or their prey. This initial menace almost invariably dissolves into a friendly encounter or submissive appeasement when pack numbers converge. In the meet, aggression takes the form of an increased tendency to gang up against individuals as the group becomes more excited. Perhaps early conditioning by adults influences each dog's search for the "camouflage" of at least one partner, but I have had the distinct impression that the formation of temporary ritualized alliances reduces the chances of being mobbed and that the joining-up process encourages a unified embarkation on the hunt.

Mobbing during the meet seems to exert most pressure against dogs that are unfit for the hunt. For instance, if any animal is lame and therefore cannot keep close to a running partner it may become isolated. Estes and Goddard (1967) have pointed out that such an individual tends to be seriously mobbed and subjected to the same sort of treatment as a trespassing hyaena. Wounded hunting dogs have been reported to be attacked and even killed and eaten by their fellows (Smithers, 1966b). The contexts for these killings have not been recorded but they are more likely to take place at the meet or perhaps the kill than at any other time. If these rare instances of killing and cannibalism are a possible outcome of mobbing, the behaviour can be seen as selection against individuals that fail, for any reason, to form close group alliances and thus tend to become identified as outsiders, like a hyaena. It must be remembered, however, that mobbing is an almost daily occurrence and its paradoxical function may actually be to promote alliances for the mobbed. The following incident may illustrate how this works. I was watching a pack that was still resting in late afternoon on the site of their morning kill, a newborn gnu. Two males had roused themselves and were running round side by side in the first stage of the meet ceremony. Suddenly they started to attack a rather small-sized female that had been resting on her own. Her whines of distress apparently drew a quick response since an adult male that had been lying behind the males immediately got up, ran over and passing the males by, turned and, with a token touch to the female's muzzle, threw his body down by her side. Immediately both animals started to twitter and from their prostrate position drove up very aggressively at the male pair, upon which the mobbing ceased. The male and female now rose but they kept close together trotting excitedly with their body and heads parallel and low-slung; after circling the waking pack they confronted the same male pair that had now found a remnant of the kill. This time the male and female simultaneously threw themselves to the ground on the other side of the fragment of skin and bone and appropriated it with more upward lunges at their contestants. The incident suggests that pairing actually emboldens each animal. (Certainly the confident demeanour of dogs in a group is a complete contrast to that of a lost solitary animal, which hoots plaintively and moves with nervous searching gestures.) Both sequences also showed the paradox of a submissive body position serving coercive ends. Mobbing may have a

similar function or originate in an extension of the aggression that makes puppies bunch. If cries of distress induce social activity and mobilize the pack, then mobbing may have the function of provoking this beneficial situation.

Most of the vocabulary of adult dogs can be referred to juvenile calls. The whining that seems to elicit the "rescue" just described originates from squeaky distress calls made by very young puppies, where it is often associated with bird-like twitterings that are essentially food-begging calls. A loud broken whine by an adult calls the young out of the den. The association of food (twittering) with appeasement (whining) is striking but twittering has acquired a more general connotation so that it appears to accompany intense social activity in the pack, at the meet, on the kill and/or while mobbing hyaenas (when it may be interspersed with whines). A higher level of excitement is expressed by yelps. These are also associated with the anticipation of food but have an aggressive connotation as they are uttered by hunting dogs during the chase and by younger animals running to meet the gorged hunters returning from a kill. As in domestic dogs, yelping is probably a low intensity bark; but barking is more purely aggressive and is not linked with food. Any startling noise, an encounter with lions, hyaenas or people, may be greeted with a harsh deep bark and Kühme (1965a) heard an exchange of peculiar barks when two strange packs met in Serengeti.

An important adult call with juvenile origins is generally uttered in the form of a series of eight or ten wailing hoots which carry up to four kilometres

on a still night. The plaintive hoots of an abandoned or lost juvenile elicit an immediate search from all other pack members hearing it and the carrying over of this imperative response to the adult's hooting is probably important for its function as a long-range contact call. It is heard on most moonlit nights, at which time the dogs may hunt after nightfall or else may anticipate their morning hunt by several hours. For instance, I have seen them harassing a group of roan antelopes at 3 a.m. in bright moonlight during the dry season. Kühme (1965a) never heard nocturnal hooting while the puppies were in the den, which suggests that the pack was reluctant to hunt by night at this time. During daylight, particularly on the open plains, dogs can maintain contact visually or by following scent and so do not use their voices, but a lost adult will hoot repeatedly.

It is likely that the relative abundance, the habits and the habitat of prey species as well as the breeding cycle of the dogs will have some influence on the activity of wild dogs but their hunting is normally crepuscular. The chase lasts between 10 and 60 minutes depending on conditions and prey is consumed in 5—30 minutes depending on the size of the prey and of the pack. They are active for about four to five hours in a day. They prefer to spend the heat of the day in shade but on the open plains are often unable to find shelter and are also greatly bothered by flies. It is probably to have some relief from the discomfort of heat and insects that they take advantage of wallows and, during the dry season, dust baths. In some localities they may have to face cold winds and Van Lawick (1970) described merry-go-rounds of dogs endeavouring to use one another as wind-breaks.

Grooming is rather perfunctory and consists of licking one another and themselves, some scratching with the hindleg and much shaking, rolling and squirming on the back.

Wild dogs are known to suffer from several diseases and it is possible that distemper, which is thought to have been introduced into East Africa in about 1906 (Simon, 1962) may have persistently kept populations down since that time. In the southern Kruger Park wild dogs were nearly exterminated by *Rickettsia canis* between 1927 and 1933 and the population was very slow in recovering numbers. Sachs (1968) may have discovered an important aborting agent in the presence of *Brucella abortus* in Serengeti dogs. At the time of the 1920 rinderpest epidemic in Uganda some dogs were found dead but the cause was not investigated.

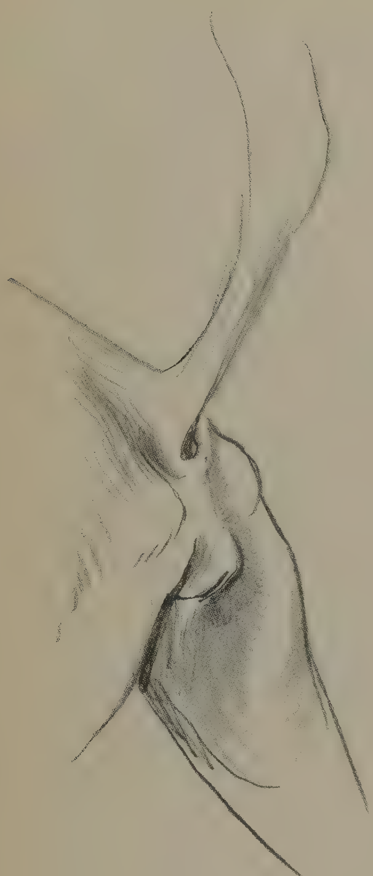
Apart from man, wild dogs have few predators because of their social defence. Instances have been recorded of lions killing wild dogs and *vice versa* and both carnivores have been seen to relinguish their prey to the other when sufficiently outnumbered or intimidated. Leopards have been seen treed by aggressive dogs and a leopard near our farm in south-western Tanzania was seen to jump down for long enough to kill two dogs before taking refuge up the tree again. They have been seen to retreat from an advancing group of baboons. Where hyaenas are sufficiently numerous and alert to arrive quickly at a wild dog kill *en masse*, they may take over the remains, particularly if it is dark, but Kruuk (1972b) has seen dogs appropriate hyaena kills five times and it is unusual for hyaenas to fight back although a rescue was once seen when the dogs attempted to kill one hyaena. Hyaenas are the main beneficiaries of the wild dogs' feeding, scavenging the bones of their

kills and, with appeasing whines, coming close to the dogs in order to eat their faeces. Schaller (1972b) was able to photograph a subadult hyaena that was permitted to feed at a wild dog kill, probably because of its highly vocal and cringing appeasement gestures.

Apart from canine diseases (the severe effects of which may be partly due to recent introduction by human beings and constant renewal from an ever-increasing reservoir of domestic dogs) man has had the most profound effect on wild dogs, principally by thinning out or exterminating wild ungulates and killing wild dogs whenever they turn to stock raiding. As *Lycaon* shows very little fear of people and never seems to learn a proper caution of vehicles it is easily shot and in this way the gamekeepers of the Queen Elizabeth (now Ruwenzori) Park exterminated this species from that region in the 1950s. Such ignorant actions may have irreversible effects, highlighting the need for informed biological counsel in the planning and running of wildlife management. (Traditional attitudes towards the larger predators are so deeply founded upon irrational fears and hatreds that scientific guidance is most necessary for policies of predator control).

Although a person approaching a den might conceivably be set upon by a pack there are few authenticated records of hunting dogs attacking people and hunters who have shot and wounded them have remarked upon their timid and unaggressive behaviour. They have been known to ignore a herdsman and attack his stock; cattle, sheep, goats and donkeys are occasionally taken, but if cattle do not panic but mill about in a tight bunch the dogs are unable to isolate an animal so that the herd comes off its encounter with only some lost tails and bitten hocks. The advantages of bunching against predators, particularly hunting dogs, is widely appreciated by pastoral people and their cattle generally move and sleep in a tight mob.

In spite of the size of hunting dog litters, which can number from two to nineteen, populations fall short of their potential, many females do not breed and there is a high mortality of puppies from disease. There are also reports of consistently more males than females in some areas. In Serengeti, Schaller estimated that one third of the dog population was less than one year old, which implies a very high rate of turnover amongst adults as well. Yet captives are known to live at least ten years. If the advantageous features of the wild dogs' biology, their communal feeding, enormous litters and intensive care of the young were not offset, the species would be much commoner that it is. The observation of packs of hundreds in the first half of the nineteenth century by Gordon Cumming is a startling contrast to the contemporary pattern of small packs spaced very widely apart. The reconciliation of these contrasts has consequences for our understanding of wild dog society and population dynamics. The giant packs were probably directly dependent on the vast herds of springbok. Were the packs temporary aggregations coming together to follow the springbok when they concentrated or migrated? Temporary or not, the former existence of big packs implies that barriers against the formation of large social units are not behavioural; in which case why are similar concentrations not seen in Serengeti, where gnu and gazelles could probably withstand the extra predation? How does disease affect the dispersal and dynamics of hunting dog populations? These and many other questions remain to be answered.



Hunting dogs breed throughout the year in East Africa but breeding peaks or seasons have been suggested for South Africa in April—June (Stevenson-Hamilton, 1950) and May—July in Zambia (Ansell, 1960b) while Schaller suggests March and April in Serengeti.

Since packs have to adopt a more settled life for nearly three months while the young are being reared in the den, the most important considerations are likely to be that prey should be reasonably close and abundant at that time, that dens should be secure from floods or predators and that the first months of the youngs' life should take place under optimum conditions.

The gestation period is 60—80 days and Van Lawick (1970) noted that a female increased the frequency of urine marking while she was in oestrus. More than one male may copulate with her and most males show an interest in sniffing at her urine or perineum or rolling in the former.

Males can occasionally make handstands in order to project synchronized jets of urine over the female's deposit and Van Lawick (1970) saw a dominant male monopolize this superimposition, and this dog kept the oestrus bitch away from too close an association with the other males. He also saw a dominant mother exercise a similar prerogative for urine marking the vicinity of the litter's particular hole.

Kühme (1965a) noted that whenever a weaker mother attempted to carry, call or suckle her young while in the presence of the dominant mother it was liable to be threatened by her and the two later competed in stealing one another's pups from their neighbouring holes. It is interesting that hunting dogs should reserve competitive behaviour and show signs of a hierarchy over the sharing of mates or puppies but not over food (although struggles while tearing the kill to pieces sometimes verge on tests of dominance).

Shortridge (1934) described dogs taking grass into their den for bedding. The site is usually an *Orycteropus* hole wherein the young are born blind and almost naked. They make brief emergences from the hole shortly after their eyes open at the age of two to fourteen days and their growth is very rapid. They start to be fed with regurgitated meat at the age of one month, after which the female's copious milk supply begins to decline rapidly until she is quite dry six to twelve weeks after giving birth.

For the pups both sucking and swallowing meat are very rapid processes seldom taking more than a minute. Although the mother or feeder is pawed and bitten by the jostling crowd, there is no antagonism between siblings and in the largest litters there may be more pups than the mother's twelve to fourteen teats, in which case the extra pups tug at her mouth instead.

The resemblance between the action of sucking and ingestion of regurgitated meat is more than accidental; for nipple sucking and mouth-tugging gestures remain interchangeable even when they appear in the adult greeting rituals accompanied by similar begging gestures.

Early weaning seems to blur distinctions between adult and infantile feeding pattern, for adult dogs of both sexes commonly attempt to suck lactating females. It is perhaps because feeding on regurgitated meat is not sharply differentiated from sucking that the behaviour patterns that accompany the parent—young relationship are more easily kept intact.

The mechanism underlying the hunting dogs' remarkable social life is

based simply on the carry-over of the juveniles' collective dependence on their parents and seniors into adult life. Because there is no clear break between the feeding patterns of infancy and adulthood, any dog can assume its juvenile role according to the needs of the moment. Thus the sucking adult, shortly before this infantile impulse, may have played its parental role as hunter and feeder. The suckling mother will herself beg like a puppy for meat and then regurgitate it for her puppies an hour later. Even the puppies can become feeders as Kühme (1965a) saw a six-week-old pup regurgitate and share its food with another.

The remarkable system of interdependence that the dogs have achieved seems to be the product of a continuous switching by every dog from the role of provider to that of dependent.

Many of the constraints and licences that accompany the original role can be recognized as playing a function in hunting dogs' social rituals. For example, the supplicants' pawing and biting are aggressive but their objective is to coerce rather than drive away. Likewise the adult's aggression towards the young serves to keep the litter together. These two modes of aggression provide dogs with a means of coercing their fellows whether they are playing a submissive or assertive role. In both instances there are built-in restraints and so damaging bites are avoided.

During food-begging both the feeder and the fed tend to express aggression at some stage, the latter in demanding to be fed and the former in having to repel further begging because of its empty stomach. Paradoxically, the feeder often has to assume the low-lying posture itself to drive the supplicant away.

When the pups are very young, all members of the pack display maternal behaviour and the male of a captive pair has been seen to lick and mouth pups immediately after birth and before the mother carried them into her shelter. Van Lawick watched all pack members, but particularly females, participating in the carrying of young back into the den before nightfall and he describes the frenzy of greetings when the pups first emerge from the den, adults rushing up to flip the pups on to their backs and lick their bellies. The males often carry very young puppies and press their chins with retracted lips down upon them. In fact males eventually become more tolerant of juveniles than females, which seem to lose interest in their young by the time they are four or five months old. (Kühme, 1965a, Estes and Goddard, 1967).

Estes and Goddard (1967) found a pack of six adult dogs with nine puppies in which the mother, the only female in the pack, died. After pulling her carcass out of the hole the five males thereafter fed and reared the five-week-old pups themselves. Kühme saw a pack depart on a hunt in which one male set off but then returned to the pups in the den. The mother had watched him attentively and his disappearance into the hole seemed to release her and she ran off after the departing hunt.

Counting the number of times the mother stayed with her young while the pack was hunting, Schaller (1972b) saw her remain in 23 out of 32 hunts and she was sometimes accompanied by other dogs. Although the mother, other guards and lame dogs left behind are fed, it is clear that the mass of puppies provides the principal stimulus for the hunters' return and the regurgitator is drawn towards them. The adult guards often join the litter to benefit from this, although they also beg themselves. Both regurgitating hunters and suckling mothers prefer to feed the young outside the hole.

By the time the young are two months old they have acquired the bold adult markings, their ears have become disproportionately large and their legs and muzzles have lengthened to near adult proportions. They now run out to meet the returning hunters, yelping and wagging their tails as they go; gradually they increase their range until they start to arrive at the nearer kills. They still expect to be fed but soon learn to feed directly off the carcass, bullying the adult hunters so that they are forced to stand back while the pups feed. The circle of hungry adults meanwhile drives off hyaenas and jackals. Once the pups start to discover kills the time lag between the adults leaving for the hunt and the young going out *en masse* diminishes and eventually their response as a juvenile bloc disintegrates in the milling excitement of the meet. It is at this point that they become members of the pack rather than members of a litter, although Kühme has pointed out that they will continue to stick together at times of tension beyond the age of five months.

Young hunting dogs spend much of their time in play. Frontal fights in which the antagonists rear up on their hind legs tend to develop out of pawing movements associated with mutual mouth-tugging, and Kühme pointed out that this game is never associated with meat, whereas the circular chases which are commonly participated in by all the litter are usually set off by one pup carrying a bit of carrion. In this game the sides and hocks of siblings are bitten at and they are particularly prone to chase one another's tails, biting at the white tip, which suggests a close association of this conspicuous flag with the joys of the chase.

While the pups are very young hunting tends to be restricted to a range of about two km around the den and the entire range of a breeding pack was estimated by Kühme to be 15—200 sq km. However, once the young are fully mobile, generally before they are three months old, the den is abandoned (often quite abruptly) and the pack resumes its nomadic existence.

Bat-eared Fox (Otocyon megalotis)

Family Canidae
Order Carnivora
Local names
Kipara (Kichagga), Nchenjeji (Kigogo), Mchutu (Kikomo), Bili (Kiramba), Bii (Kinyaturu), Ameguri (Karamojong)

Measurements
head and body
47—66 cm
height
30 cm
tail
23—34 cm
weight
3—5·3 kg (females may be heavier than males)

Bat-eared Fox (Otocyon megalotis)

Race

Otocyon megalotis virgatus

In spite of its extraordinary dental specialization (illustration, p. 11), this little animal with enormous ears is recognizably a fox. Its slender legs and sharp little muzzle give it a delicate air, while its handsome tail is almost as big as the body. The very conspicuous tail and ears are obviously important means of expression for the foxes and these extremities are seldom quite still in any sort of social activity. In addition to their value for signalling, the ears function as reflectors, gathering subterranean insect sounds, while there is evidence that the tail can in emergency serve to distract predators from the body.

Like the racoon, *Procyon*, the striped hyaena, *Hyaena hyaena*, and many other carnivores, *Otocyon* has a black face mask which Kleiman (1967) thinks is related to social grooming. The fox's face is the area that is most frequently nibbled at and the ears, legs and tail are also attended to, suggesting that black is a focus of attraction. Being on all the extremities, it also outlines the animal and thus emphasizes any posture that it takes up. There is an annual moult and the new coat coincides with the cold season in southern Africa (Smithers, 1971).

The bat-eared fox is found on well drained soils within the semi-arid Somali zone (another race occurs in south-western Africa). It favours fairly open acacia woodlands and grassy plains.

In a sample of fifty stomachs Smithers (1971) found the adults and larvae of *Isoptera* and *Coleoptera* constituted the most frequent and abundant items. Termites were the only contents of six stomachs and filled more than half of five more. In Botswana the most commonly eaten genus was *Hodo-*

termes. Small rodents appeared twelve times, reptiles eight, and fruit nine times. Some grass was recorded in about half the stomach samples.

The three stomachs that I have examined consisted wholly of termites and some vegetable and soil debris. Bothma (1959) noted termites predominant in eight stomachs although other insects, a gecko and bits of vegetable matter were also found. Beetle larvae are especially important in some localities and seasons. Apart from ants, millipedes, scorpions, grasshoppers, crickets and beetles they are also reported to eat certain tuberous roots, groundnuts and fallen fruit. Lizards, small snakes, gerbils and young birds are caught or run down in a very fast well manoeuvred dash. Shortridge (1934) observed a tame one that never bothered older poultry but was quick to snap up new chicks. The diet of pet foxes seems to reflect more the eating habits of the owners than anything else but it is interesting that honey, butter, bananas and papayas were greatly favoured, while mangoes and pineapples were rejected by Loveridge's captive (1923). On three occasions, Leakey (1969) saw these foxes appropriate to themselves pigeons that falcons had killed but were unable to carry off the ground where they had fallen. Though wild foxes can go for long periods without water, captives drink regularly.

Hunting for food is a strictly individual affair. Both rapid digging and eating are essential to success and no distraction or competition is tolerated, so foraging foxes are generally well spaced and any close approach while another is feeding elicits snarls and growls with the ears laid back, flat on the neck. Pet foxes extend their possessiveness over food to people and will threaten anyone who approaches them while eating. They also exhibit an intensely exclusive digging impulse which can happen apparently quite spontaneously at any time and place with equally fierce reactions against any interference (Turner, 1968).

The advantages of rapid digging, both for food and shelter are obvious and fits of furious digging presumably reflect the importance of this as a built-in activity quite independent of hunger or fear. Digging for food is conducted at a very rapid pace but with sudden pauses, nose to the ground and ears cocked forward and out so that they cap the hole. The hole may then be neglected or further rapid digging may reveal a grub or termites; foraging foxes dart here and there and if they encounter other animal species they will often provoke them by repeated chasing, snapping and fleeing.

Ewer (1973) relates play in this species to escape behaviour but it seems to me that two distinct advantages can accrue from harassing other animals. One is that they may relinguish food, like the falcons mentioned earlier, the other, more important, is that competitors or simply "disturbers" of the hunting grounds and home burrow are chivvied away. What looks like play could in fact be functional behaviour. Thus it is not unusual to see a group of foxes clapping their teeth loudly and waving their arched tails as they chase off guinea fowls. Loveridge (1951) describes the reactions of a free-ranging tame fox to various animals that might be regarded as equivalent to competitors.

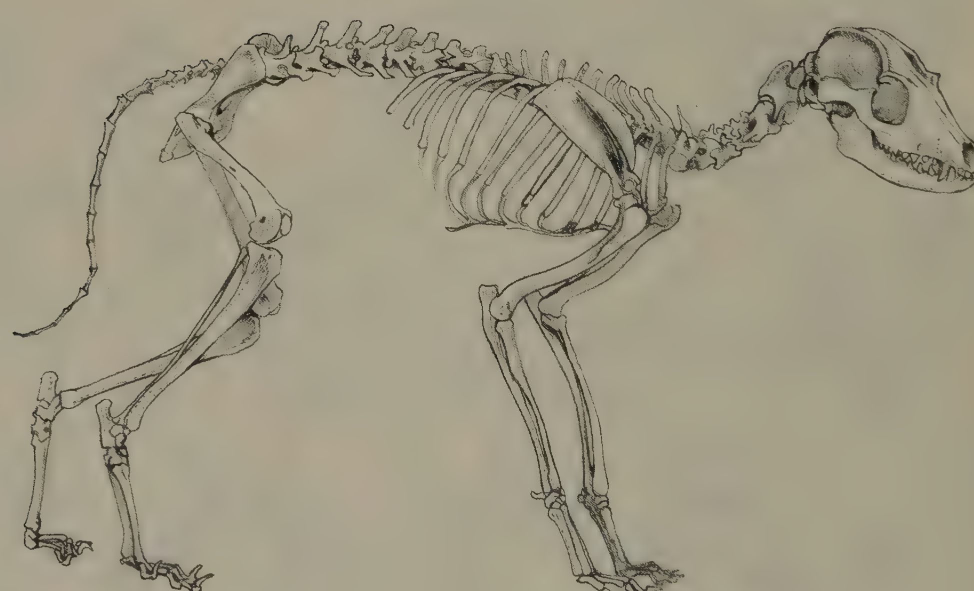
> "The fox lay crouched upon the driveway until a big dog baboon, walking slowly towards him, came within a couple of yards; then Kip sprang up and rushed straight at the larger animal. The baboon, loping easily away, would look back over his shoulder at the pursuer he could so easily kill. Many other baboons were close by, either watching the play or grubbing among the fallen leaves and branches in the vicinity. . . . Another of his pastimes was to wait till the pigeons were on the ground, then charge among them. Indeed, he loved chasing anything but would hurt nothing. Even the chickens seemed

aware of his harmlessness, for they paid him scant attention, whereas they went into hysterics at the sight of a serval kitten."

This animal also chased pigs, dogs and people.

On the whole, *Otocyon* are rather quiet animals but they sometimes utter rapid repeated wails. Shortridge (1934) described this thin call as resembling that of a common fox and he noted the mother calling and being answered by the young and a cry of distress when trapped rendered as "Ha-ba-wa-wa". The juvenile call is a mewing, whistling note which develops into a contact call between adults which sounds rather bird-like. Turner (1968) described a sigh "out of all proportion to her size" uttered by her captive when it settled down to sleep.

Otocyon spend a great deal of time nibbling one another while, according to Lamprecht (personal communication), licking is a rarer form of grooming. Although grass seeds and burrs are easily picked up by the thick, rich fur and fleas and ticks are not uncommon parasites, the grooming seems to be primarily an attribute of their social life. They keep their burrows very clean and excrete away from the entrance.



In the middle of this fox's back there is a parting in the longer fur, beneath which is a patch of shorter fur which might cover a glandular area. *Otocyon* frequently roll on the ground with quick side to side rolls and Kleiman (1966)

has remarked that it would be interesting if the evolution of a new scent gland were associated with a modification of the normal canine rolling pattern.

Bat-eared foxes are crepuscular and nocturnal feeders, but they are frequently awake outside their holes for all but the hottest hours of the day, particularly the young. They become most active in the evening and I have encountered them until about midnight and then again in the early hours.

Flying low over Masailand in a balloon one morning, I was surprised at how active and how numerous these foxes were in the lightly wooded acacia savanna during the hour after dawn, at which time they were evidently still hunting.

The burrows of *Otocyon* are shallow and, if not self-dug, may be modified spring hares' holes. They usually have several entrances and can be inhabited by up to ten foxes. During the brief but often heavy rains in their habitat these holes may get flooded, although the water soon drains away in the sandy soils they favour. It is interesting that captives have been reported to be frightened of rain and particularly of thunder claps (Turner, 1968).

In Serengeti, the normal and most frequent social unit is an adult pair and their offspring, usually numbering three to five, but Lamprecht (personal communication) watched one group of two pregnant females that lived with one adult male. A den containing eight animals that was watched by Van Lawick (1970) contained two adult females and their litters, which sucked indiscriminately.

The male marks the area surrounding the den with urine. He may lift one leg or squat, but the deposits are never aimed at a stem or branch but are directed on to the ground. The females only urine-mark just before and during oestrus. Smithers (1966a) described adults depositing scent and urine far from the burrow and usually under the shade of a bush. Dung was deposited in the same place only two or three times; a captive also used small middens away from the house, where it was very clean. Aggression between foxes is expressed by snarling and growling with flat ears and an erect and fluffed out tail exposing the reddish underfur near the base. Like dogs and jackals, young animals display submission by falling on their backs and exposing the belly while wagging the tail and licking with the mouth slightly open and lips drawn back.

In the Utica Zoo, Rosenberg (1971) saw a male mate up to ten times daily over a week. The female showed no swelling of the vulva but the male started showing a special interest in her the day before copulation started. Rosenberg thought that gestation was 75 days, which is unusual for so small an animal. This female had her next oestrus nearly ten weeks after parturition. Smithers (1971) found gestation ranged between 60 and 70 days.

Several records of births from Tanzania are for October (early rains) and Shortridge (1934) stated that they are born in the rains in south-west Africa. In Karamoja, cubs have been recorded in March and it is possible that bat-eared foxes may produce two litters a year as the young are adult-sized and independent at six months.

Two to five young are born at a time and litters may be synchronized and shared by two females. It is not unknown for very young cubs to be found abandoned, possibly through flooding of the burrows.

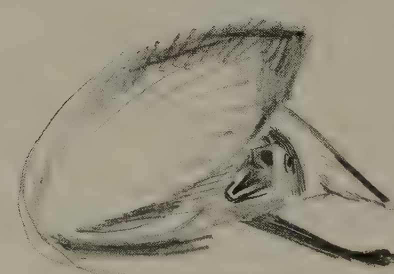
Development is very rapid, the ears growing particularly fast. Within

about a month of birth they will eat insects and shortly afterwards are weaned. Loveridge (1951) reared two cubs.

> "During the first few weeks they saw to it that I rose once or twice each night to give them their bottles, for when hungry they announced the fact with sibilant whistling calls. At all times they could produce a large and varied repertoire of noises to scare unwelcome visitors. Except for a couple of hours at noon, when they took a siesta, the cubs were lively all day. This was apparently normal, for at Saranda I had been shown a burrow around which eight foxes had been seen basking one sunny morning. Cubs that are lively by day and sleepy at night probably suit parents who have to go out foraging at night. Later my cubs liked to be out after dark, particularly in bright moonlight."

Before they are weaned, the young accompany their parents and the cubs' seizure of the parents' insects is tolerated during the brief period of learning to find their own food.

This period is likely to be a crucial one for the survival of the young, which must be vulnerable to attack. Wilhelm (1933) stated that they are often killed by leopards in south-west Africa and Kruuk (1972b) twice found foxes that had almost certainly been killed by hyaenas; but their greatest danger comes from eagles. I have been fortunate enough to get a bird's-eye view of foxes fleeing an aerial "predator" while flying over them in a balloon; they zig-zag furiously to the nearest den with their brushes flailing over their backs. One arrived at a blocked hole just as we sailed overhead and he crouched in the depression peeping out beneath the protection of his tail.



Had I been an eagle, the sequel might have resembled a skirmish that was observed by a game warden at Makindu between a martial eagle and a bat-eared fox.

> "The fox lay on its back with tail erect and flailing back and forth while it snapped at the upper parts of the eagle's legs, bringing notes of pain from the bird, which soon afterwards quit, upon which the fox got up and scuttled into a nearby burrow." (K.G.R.)

In flight, when crouching for shelter and when the fox is actually engaged with the raptor, the distracting role of the tail seems to be important and the associated behaviour probably of very real survival value.

This fox is rather vulnerable to dogs and for this reason and because of cultivation and hunting for its pelt it is declining in settled areas. In Karamoja, the tail is attached to the traditional head dress as a tassel.

They probably suffer from most canine diseases and Leakey (1969) noted substantial fluctuations in the numbers that could be seen around Olduvai gorge from year to year.

Mustelids

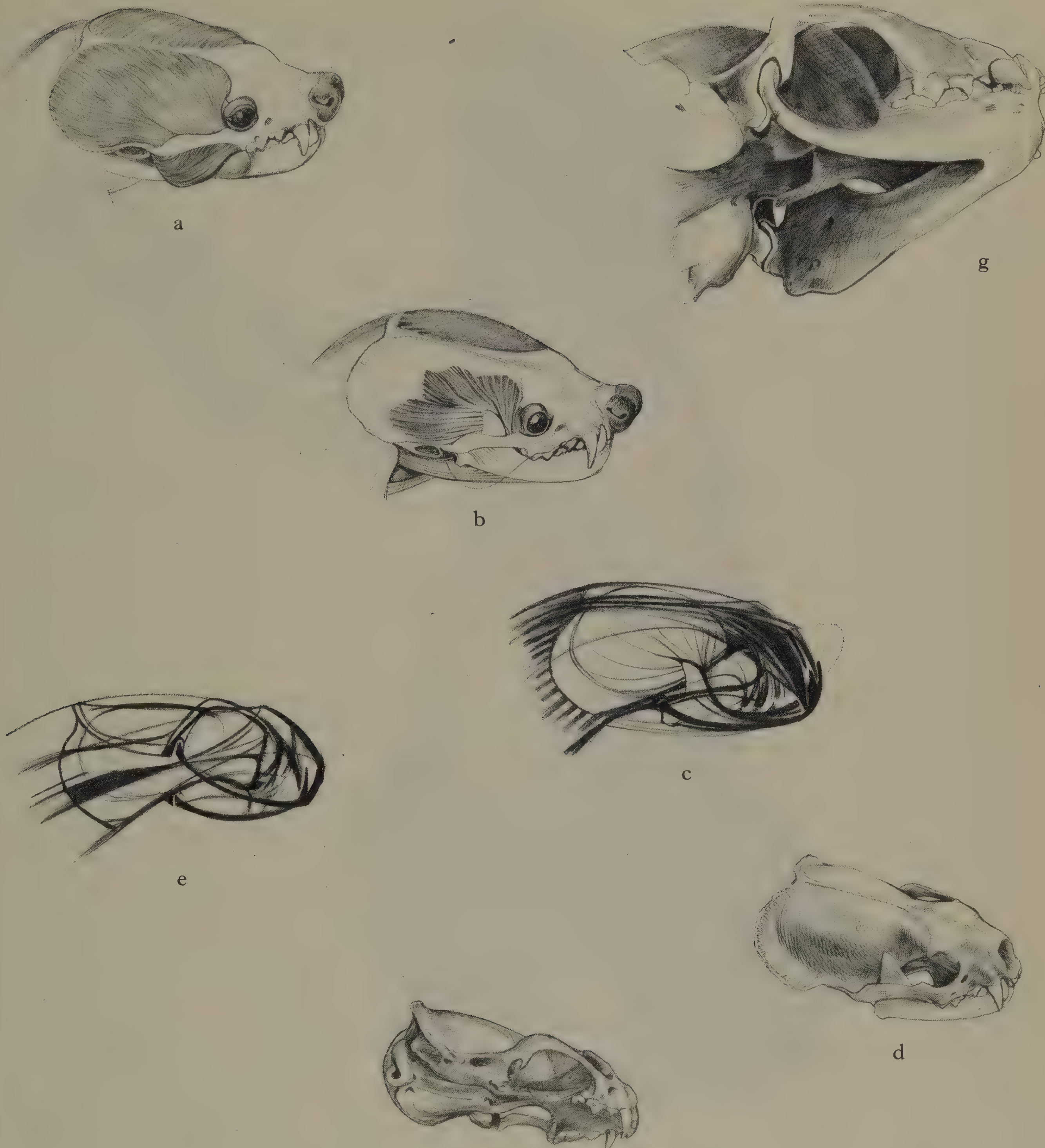
MUSTELIDAE **Mustelinae**
Lutrinae

Members of this family of carnivores are not very well represented in Africa, being primarily inhabitants of temperate Eurasia and North America, where their niches are often equivalent to those occupied by the numerous viverrids of the Old World tropics. In Africa, there is some evidence to suggest that temperature may influence the relationship between some of the six rather specialized mustelids and their potential viverrid competitors. Thus the clawless otter, *Aonyx*, lives mainly in lakes and large rivers but is also found in small streams at higher altitudes where the marsh mongoose, *Atilax* (see p. 207), is usually absent. The zorilla, *Ictonyx*, and the striped weasel, *Poecilogale*, both tend to be more abundant in the highlands where there appear to be fewer of their usual competitors, mongooses.

Although the African representatives are as diverse as the otters, honey-badger, striped weasel and zorilla they have a common tendency towards long bodies, relatively short legs with specialized and dexterous forepaws and large brains. All have well developed canines; as the toothrows have reduced the number of teeth, the jaws have shortened and apart from the canines the dentition is relatively weakly buttressed; there is a conspicuous development of the temporal muscle while the masseter is small. These peculiarities suggest that the original speciality of the mustelids was the killing of small animals with the canines. The pre-eminence of the temporal muscle is linked with the extra development of the glenoid processes around the condyle of the lower jaw. The function of these modifications is to allow the canines of both jaws to clamp together without any dislocation or torque at the articulation. As the temporal and neck muscles take the strain of the prey's struggles, crests and overall areas of attachment on the cranium are appropriately large.

Contemporary mustelid genera have secondary specializations to eat crabs, catch fish and excavate holes. Aquatic and fossorial ways of life have tended to obscure common origins and there are few intermediate fossils to help. A reconstruction of the families' evolution must be largely deduced by comparing living end-products of an almost world-wide radiation.

Miacid fossils from the early Oligocene may include ancestral mustelids but at this time they can scarcely be distinguished from the other carnivores. *Lutra* turns up in the mid-Pliocene deposits at Wadi Natrun and *Eomellivora* in the Eurasian Pliocene but fossils from the Miocene and Pliocene deposits are not considered to be forerunners of the living mustelids (Simpson, 1945). The largest of these fossil forms, *Megalictis*, was as large as a bear but the great majority of mustelids have always tended to be relatively small and the terrestrial types catch their prey by skill rather than speed. Most of them have a long, low-slung body and rather tubular skull form.



a–f Poecilogale head: a, b, musculature; c, e, stress and reinforcement lines; d, f, skull surface features; g, *Mellivora* skull to show glenoid processes around condyl.

The anal scent glands are very highly developed in this family, notably in the zorillas, polecats and American skunks. As a defence against predators this attribute is linked with small size. The secretion is not only nauseous but is acrid to taste so that predators penetrating the first defence meet the second if their mouth comes into contact with the animal's tail end; instead of

fighting the zorilla and other mustelids often sham death at this stage. It is interesting that the larger ratel, *Mellivora*, which is well able to give a good account of itself, and generally does fight very fiercely, may quite unpredictably choose to sham death, which suggests that it retains behaviour elements that were more appropriate to its smaller ancestors. Glandular secretions are common to almost all mammals, but the mustelids have gone beyond the original function of extending the body's occupation of space and thus simultaneously conveying a sense of confidence to the owner and information on the individual's identity and condition to conspecifics (see p. 6). The repelling properties of the zorilla's secretion are unquestionable but so far as is known the stink is directed only against enemies and tame captives have been reported to be quite inoffensive pets. There is evidence from other mustelids that the individual's disposition at a given moment may alter the properties of the effusion. The ratel uses its anal secretion to mark its surroundings and also friendly beasts, but keepers who have been subjected to this particular expression of affection have not described being offended by the smell (Sikes, 1964). Yet I can vouch for the stink of an angry ratel being truly unpleasant. Like the zorilla, the ratel's small ancestors probably protected themselves in this way but this secondary use of the anal glands acquired a tertiary function when the suffocating properties of secretion produced in a state of excitement were turned to overcome the defences of various well protected colonial insects, notably ants, termites and, above all, bees. This allowed the ancestral ratels to open up a new food supply for which there were scarcely any competitors.

The size and body-build of the contemporary ratel are appropriate to the task of breaking up the hardened soils and hollow trunks that encase their favourite foods. The size of the body has perhaps increased as a direct result of entering into this new niche and the stocky proportions of the body have led various authors to assume that the animal is related to the Palaearctic badgers or the wolverine, *Gulo*. This is not so and de Winton (1902) correctly described it as a giant weasel modified for digging and quite closely related to *Ictonyx*.

A Pliocene mustelid thought to be related to the ratel was described from Odessa by Zdanski (1924) who named it *Eomellivora*. This form has a hyaena-like dentition which has similarities with that of a newly found fossil from the Pliocene deposits at Ngorora. The new fossil resembles *Mellivora* very closely in cranial characteristics.

The large brain of the Mustelidae might be linked with the high degree of co-ordination and dexterity that they exhibit. Otters are notoriously adroit with their fingers but it is not generally appreciated that most of the other mustelids are also capable of considerable ingenuity and manual dexterity. (The evolution of the Lutrinae is considered later p. 104.)

The family is generally regarded as having originated in forest habitats (where most of the temperate zone mustelids are still found) and it should be mentioned that scent-marking is particularly common and well developed in many forest mammals.

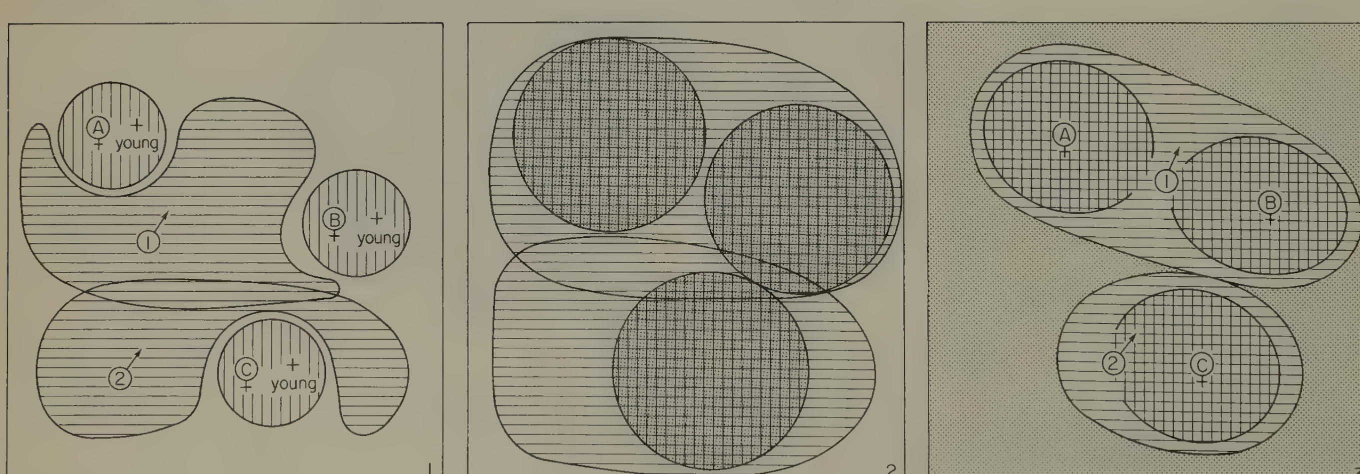
Most of the terrestrial mustelids hunt by scent and pounce on their prey with a bite of vice-like strength; those that prey on vertebrates then tend to use their feet to yank the body of their prey and thus dislocate its spinal

column. The pounce is made at close quarters. In the case of the clawless otters discovery is often by touch, but most of the mustelids direct their final attack by sight and the movement of their prey triggers off their very fast killing responses. One product of this is multiple killing—weasels, zorillas and ratels often kill a whole party of birds or rodents, and otters sometimes kill numerous fish in quick succession. This in turn can lead to hoarding. *Poecilogale* carry home their mice. *Lutra* sometimes land a small pile of fish and *Mellivora* has been seen carrying away honeycombs and other prey to hide or bury.

Not a great deal is known about the social life of African mustelids. As has already been mentioned they rely a great deal on scent for communication although they can be fairly vocal at times, and most species display dramatic postures in which positions of the tail and exposure or concealment of the neck appear to have special signal value (see p. 76). All species tend to be solitary or form pairs, but aggregations in excess of a simple family have occasionally been reported in *Mellivora* and *Aonyx* and more regularly in *Lutra maculicollis*.

Apart from specific food and habitat requirements the density of a mustelid population is probably regulated by the intolerance of females during the months following whelping and of males during the mating and courting period. Subadult animals take the brunt of these periods of exclusion and are probably forced into a peripheral or nomadic existence until they find themselves an area of their own (see diagram). In Sweden, Erlinge (1969) found that the number of female otters breeding in a district was strictly

Mustelid dispersal phases



ad ♂ ranges
ad ♀ ranges
juvenile or subadult ranges

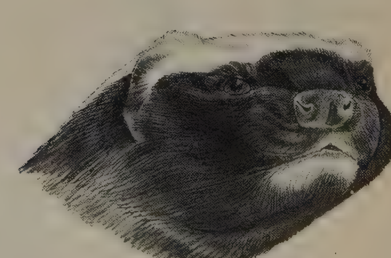
1. Infancy or "female intolerance" phase
2. Juvenile or "social" phase
3. Mating or "male intolerance" phase

limited and his observations suggest how population densities may be regulated in other mustelid species.

> "One year three females bred in a district. The third female settled outside the areas regularly occupied and a less favourable site. A tremendous marking activity occurred in that area, indicating that the density had reached a critical level. Moreover, available data indicate that in otter populations with a high density some females do not breed every year. This might be due to the territorial organisation."

The females of several mustelids have been observed to make special calls when they come into season and this probably supplements scent trails as a means of bringing pairs together. In spite of the female's being receptive at this time, mustelid courtships are rather violent affairs with the female tending to fight back and the male holding the female down by the nape of her neck and even dragging her about. He is careful, however, not to bite deeply. It is perhaps the need to overcome female aggression that ensures that the males are slightly larger and heavier. Without the sexual stimulus to counteract her repulsion, the female's aggression drives the male off before she has a litter. It is likely that secure shelters in optimum feeding grounds are monopolized by the females and it is in well hidden retreats that the young are born. Mustelid young need several months of intensive mother care, during which time they tend to stay well hidden. All members of this family are extremely playful, particularly when young. Their games derive mainly from food chasing and manipulating. Mating and, later, hunting take up relatively short periods of time so that an important function of play in such circumstances is to reinforce hunting techniques. In the security of the home area or in the burrow itself, the energies of the growing young can be expended in play while they are learning and improving the co-ordination and speed of movement that are the hallmarks of the mustelid family.

Mustelines



Mustelinae

The African mustelids are subdivided into two subfamilies, the aquatic and highly distinctive otters or Lutrinae and the terrestrial mustelines, the characteristics of which have been outlined in the preceding profile.

Zorilla (Ictonyx striatus)

Family Mustelidae
Order Carnivora
Local names

Kicheche (Kiswahili), Ucheche (Kirwa), Kichete (Kimbungu), Tegaruhende (Runyankole and Lunyoro), Gralumende (Kipangwa), Kitagna (Kigare), Mukhuluwandurisi (Lubukusu), Ikikalangasa (Kinyakyusa), Mongashiet (Sebei), Olpilis (Masai), Goris abahana (Kiliangulu), Eurungorokapolon (Karamojong), Urungro (Turkana), Okela (Lwo and Alur), Kala (Kidigo), Kidzima (Giriama), Keye (Kinyamwezi), Lingusila (Kimatengo), Lunkwiri (Kirangi), Lonzi (Kiramba), Longe (Kitaita), Lwenge (Kikamba), Kainai (Kiiraqw), Kipoporu (Kichagga), Simbulu (Kisumbwa), Njoire (Kikuyu), Eshimuna (Luhya), Mukuzu (Kizanaki), Nyilili (Kisukuma), Suzi (Kibondei)

Measurements
head and body
34 (28—38) cm
tail
23 (20—30) cm
weight
1·3 (1·02—1·4) kg

Zorilla (Ictonyx striatus)

Ictonyx

In parts of Kenya and Tanzania the zorilla is a common sight to nocturnal travellers whether on foot or by car. The moonlight reflects off the arched plume of its white tail and beneath it the white dorsal stripes stand out against a black background and the darting busy shape is highly distinctive, both in its visual impact and characteristic movement. Even more familiar will be bundles of black and white fur lying on the roadside. Unlike hares and antelopes that meet a similar fate, dead zorillas do not seem to attract scavengers to anything like the same extent and thus lie about the roads for much longer. Even the scavenging birds of prey seem to avoid them, although a vulture may occasionally be seen picking at one. Any small animal is vulnerable to eagle owls at night, yet the zorilla makes no effort to conceal itself which may be significant. The foul smelling and caustic secretion of the anal stink glands is a proven deterrent to mammals but birds generally seem to be more tolerant of smells. One of the most noxious ingredients of the mustelids has been identified as butyl mercaptan and the American skunk has been reported to be able to deter hawks (Ewer, 1973). As the secretions of these mustelids are probably of similar composition, the zorilla may have an effective defence against birds of prey.

When the zorilla is excited, the hair on its back radiates out from a point in the centre making a long diamond shape when viewed from above, and zorillas tend to turn their back on any source of threat. With dogs the zorilla has two lines of defence. The first one is to spray its secretion, the second is to lie limp and sham death. It has been noticed, however, that the shamming zorilla will make a quick flip so that it always presents its dorsal aspect to the enemy. This presentation of the striped back towards the enemy may be contrasted with the zorilla's exclusive pre-occupation with the black underparts of their bodies during friendly interactions with other zorillas.

It is possible that the pungent irritant secretion contaminates the hair, particularly that of the tail, and this may re-inforce its visual warning implied by the aposomatic colouring (Cott, 1940). A potential predator biting or mouthing a shamming zorilla might also be deterred by texture and Shortridge (1934) notes "an electric quality" to the fur.

One other aspect of the zorilla's colouring should be mentioned, the face markings, which are highly variable. If it is important that individuals know one another then the face markings would perhaps allow recognition at a greater range than would scent.

The long sharp claws of the zorilla's forepaws indicate they are adapted to dig. In other respects the zorilla's body is that of a relatively undifferentiated carnivore. The teeth are shorter than those of *Poecilogale* and the cutting edges of the shearing teeth are less developed, and this can be correlated with a less exclusively carnivorous diet.

The small carnivore niche is dominated by mongooses in Africa, and it is interesting that only two mustelids should compete. *Ictonyx* probably includes a larger proportion of mammals and birds in its diet than *Mungos*, *Herpestes* or *Ichneumia* and unlike *Genetta* avoids eating vegetable matter,

but the dietary overlap with these and other viverrids must be considerable.

In overall range, *Ictonyx* probably overlaps most of the viverrid species outside the forests. It is present but very scarce in thicker and moister vegetation types such as woodlands and grass savannas but is common in open highland areas, particularly on dry but cold rangelands where wild and domestic stock are responsible, rather than fires, for keeping the grass down. Exposure may therefore be a key factor influencing the zorilla's ecological distribution, and allowing it to feed without competition from species that may be faster and more efficient feeders but are more vulnerable to predators, above all to raptors and owls. The link with short grass and reduced burning may be related to cover and also to food resources. Beetles and their larvae and mice seem to be important foods and both flourish in unburnt rangelands, where there is an abundance of dung for the former and adequacy of fodder for the

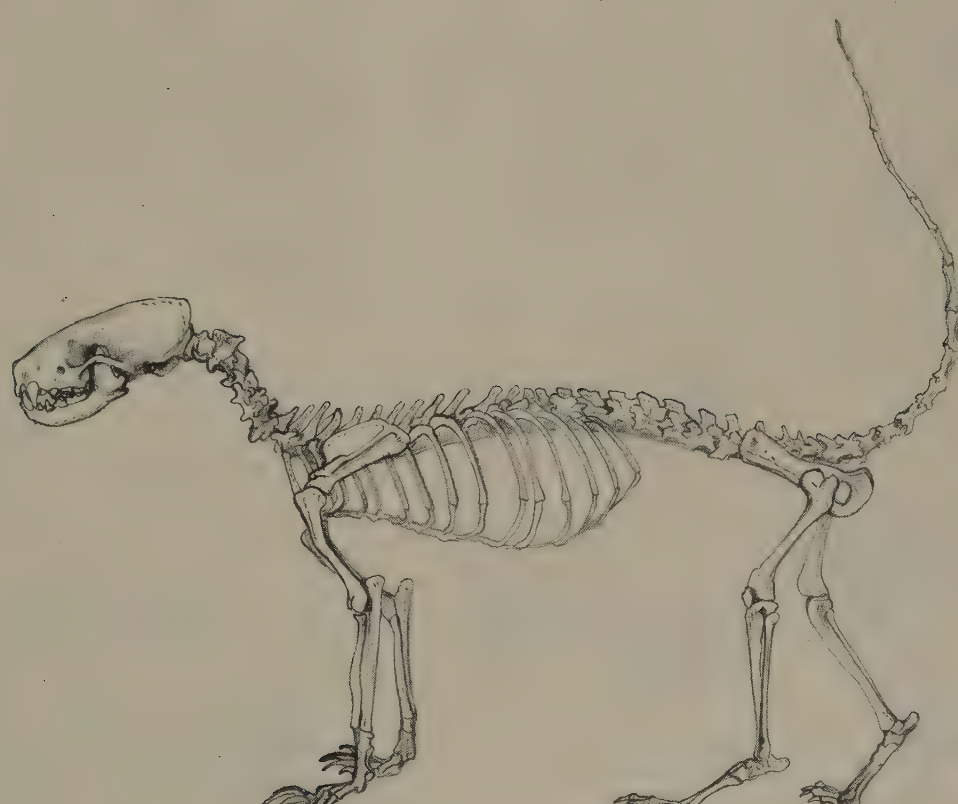
latter. Other recorded foods of the zorilla are small mammals up to the size of a hare, small and medium-sized birds, reptiles and their eggs, frogs and a variety of invertebrates, mainly insects. Food is found by scent and very often dug out of dry dung. It presents a striking contrast to *Mungos*, however, as its feeding is completely unhurried and non-competitive, whereas the mongoose must avoid losing its morsel to a fellow and eats as fast as possible.

They are almost wholly nocturnal but they are occasionally seen about during the early morning or late evening. They have been seen to swim and to climb trees, although both these activities are normally avoided.

A foraging zorilla walks rather slowly or runs along in a very buoyant trot with the back held in a firm arc but with frequent stops or reversals that are instantaneous and give the impression that the animal has quick reflexes. Sight and the sense of smell are well-developed but the latter is undoubtedly the more important. Compared to *Mungos*, they are quiet animals. They grunt occasionally and on the least alarm they growl and fluff their tail.

They do not always stand their ground but, when pestered by dogs, their growling rises to a high-pitched scream and they reverse their hunched bodies with, ultimately, a squirt of the anal glands. Since the object of this performance cannot be seen by the zorilla, it swings the hindquarters so that the liquid squirts over an arc. If this fails to deter the dog, the zorilla topples over and lies limp. The chemical defences of an adult zorilla are developed rather slowly. When the young have a head and body length of about 13 cm they start to follow the mother in a close single file. Before this they remain hidden in a burrow, which may be natural or have been dug by the mother.

Tenancy of holes seems to be temporary, although the mother is said to stick to one hole while the young are very small, unless there is a disturbance.



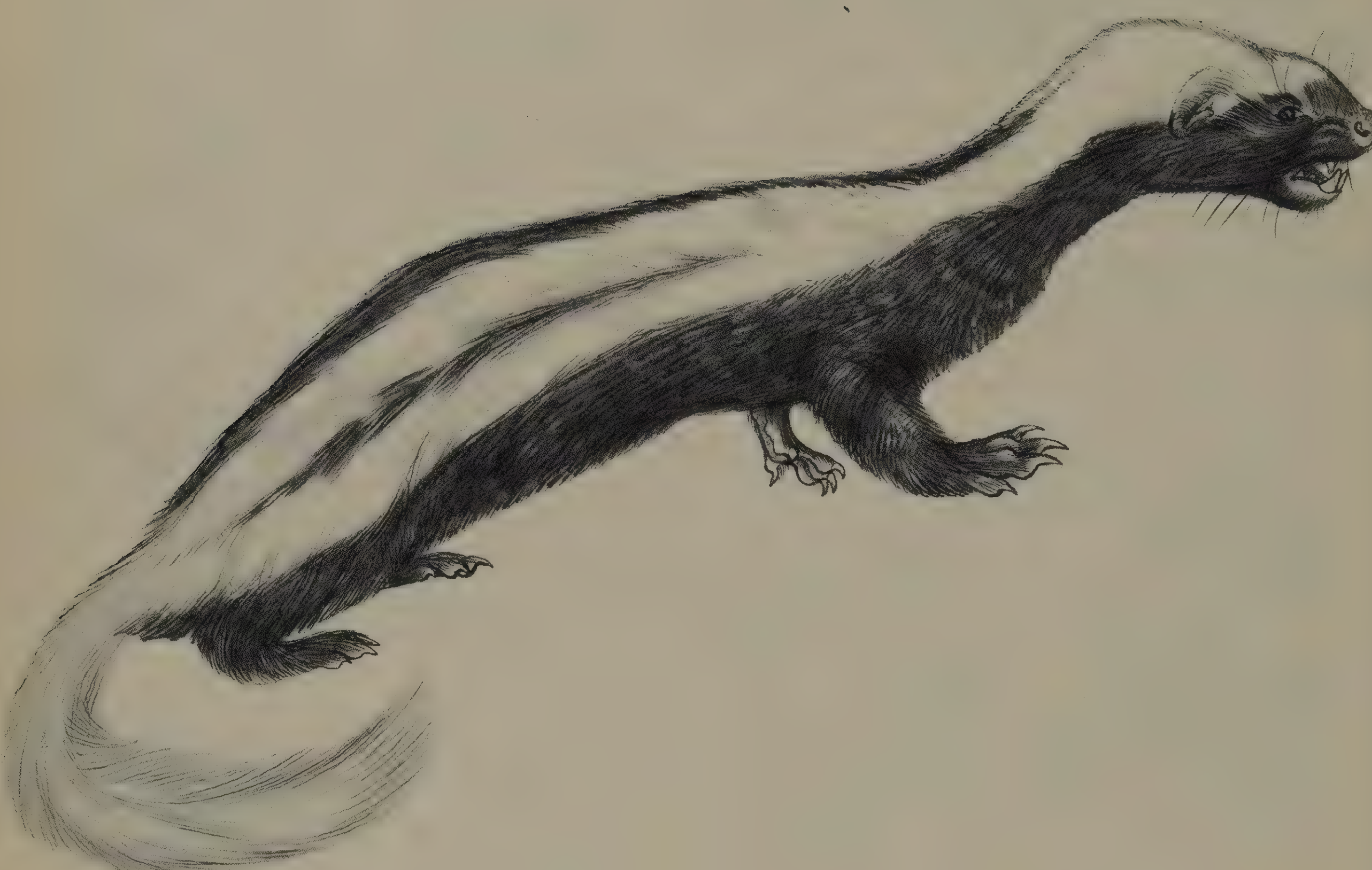
They seem to lead a fairly nomadic existence, but nothing whatever is known about their social life. Several families have been kept together in captivity and grooming appears to be very common in such groups; with pairs toppling over and presenting their bellies and particularly the black throat for intensive grooming. Such numbers are never encountered in the wild but the easy association suggests that they do not have a highly developed territorial behaviour and the home ranges of these normally solitary animals probably overlap very extensively.

Males are not generally present with mother—young groups. Several members of the family are often run over by vehicles, because none of the other animals will leave the scene once one has been hit. My own records for such mother and young casualties are two separate records near the end of February, two others in early September, one in October and a record of blind young in June.

At birth the young are blind and pink. Once they can see and run, they follow the mother on her walks and slowly learn to feed for themselves. Such groups do not break up until the young are of adult size. London Zoo has kept a zorilla for five years.

Today zorillas are probably killed more by motor vehicles than by any other agency. Their disease pathology is not known and ecological changes that might affect them can only be guessed at. They are certainly very common on the big sheep farms and ranches of the Kenya highlands. They may perform an extremely important role in pasture by keeping down the number of beetle larvae that feed on roots and grasses. In some areas, where there are no predators of the beetle and moth larvae, the entire pasture ley can be destroyed by them.

Zorillas are sometimes kept as pets and the glands are sometimes surgically removed to make them more acceptable. In contrast, Wilhelm (1933) reported that the bushmen used to remove the glandular secretion as a perfume for their own use!



Striped Weasel (Poecilogale albinucha)

Family Mustelidae
Order Carnivora
Local names

Chororo (Kiswahili), Okak (Lwo), Akakorwa (Rutoro), Kakurwa (Runyoro), Akekorya (Rnyambo), Ikikara (Kiha), Ikinyenga (Kinyakyusa), Wakaruri (Kikuyu), Kikongogo (Kihehe), Ekworiwo (Ateso), Akasumunyiga (Rukiga), Okanyamwenye (Runyankole), Kanyamulolotі (Lukonjo), Walunyele (Lubukusu), Mkunduyeye (Kinyamwezi), Limhundulu (Kipangwa), Njololo (Kisukuma), Mbulu (Kigogo), Mbilis (Masai), Lunelezi (Kisumbwa), Ususu (Kirwa), Kasolwe (Kibende), Kachongo (Kitaita), Ifuzyo (Kinyiha), Chi-ive'i (Kirangi), Lilambalwajo (Kingindo), Kwererut (Elkoni), Eurunnungorok doci (Karamojong), Ucchecheti (Kimbungu).
Note : In some areas no verbal distinction is made between this animal and the white-tailed mongoose, zorilla or genet, in spite of physical differences being recognized

Measurements
head and body
25—36 cm
tail
13—23 cm
weight
330—350 g

Striped Weasel (Poecilogale albinucha)

Poecilogale albinucha

The striped weasel is long and slender with very short legs. The underparts are jet black and the nape and tail are white, while the back has black longitudinal stripes with light stripes in between. The latter are generally white or near white but Ansell (1960) noticed that the colouring of the light stripe is unstable, altering in a living captive from light yellow to quite deep buff. He was unable to correlate such variation with age, season or any other factor. Stuchberry (1968) records that even in the short space of about six weeks the dorsal stripes of a subadult animal changed from white to a light honey colour.

As colour has been the main criterion in naming races, it does not seem useful to recognize any subspecific divisions at present but it should be mentioned that animals from western Uganda tend to be slightly larger than those from further east and south.

This species' resemblance to the zorilla, to which it is less closely related than to the plain coloured weasel and stoats of the Palaearctic has provoked suggestions that *Poecilogale* might be a mimic. It is more likely that the black and white markings of mustelids are functionally convergent. In relation to the size of its limbs this animal has the longest body of any African mammal. While walking the body is usually arched to some extent, but in faster gaits it appears almost to undulate. D'Arcy Thompson (1917) compared the weasel to a caterpillar and pointed out that light body weight reduces the effect of gravity as a force. However, when the striped weasel gallops, its back seems to arch rather less than one might suppose. The animal, instead, seems to progress by short springs that are powered by flexion in the lumbar region and synchronized hindlegs which propel the stiffer forepart of the body in a series of shallow trajectories. In describing a game played on its own by a captive, Stuchberry (1968) saw this subadult animal thrust forward off its hindlegs in the bounding movement but it failed to put its frontlegs down to take its weight and so repeatedly took the impact of the leap upon its chin, a shock that "worried him not a bit".

The weasel relies upon the power of its back for locomotion and also employs its concentrated force to help quell resistance in prey. The weasel bites its victim, usually a rodent, at the back of the neck and, rolling over on to its back, clamps part of the rat or mouse between its jaws and forepaws, meanwhile racking the victim's body with well co-ordinated kicks that are discharged by means of the powerful spasms of the weasel's long back. These kicks differ from those of a feline in that they do not rip so much as wrench, and their function is probably to help dislocate the prey's vertebral column and thus quickly render it immobile. Another obvious use for a sinuous body and short legs is travelling down rodents' burrows and, indeed, this is common.

Until recently the geographic and ecological range of this small carnivore had not been fully realized. It is distributed from the Cape to the southern Sudan and across the southern half of the Congo basin to the east coast. It may be scarce or absent from much of this vast area but its behaviour is less

conspicuous than that of the zorilla; its activity is almost entirely nocturnal and probably involves a minimum of exposure outside the burrow and its habitats are often quite thickly vegetated.

Cover may be important for two reasons. As a small and easily seen animal, it is possibly subject to predation, particularly from large owls and, more important, cover is generally essential to its prey, small rodents. Because numerous sightings have come from areas where there are many gerbils, blesmols or root-rats, it has been suggested that fossorial rodents represent the weasel's main diet and that they are specially adapted to hunt within these animals' burrows.

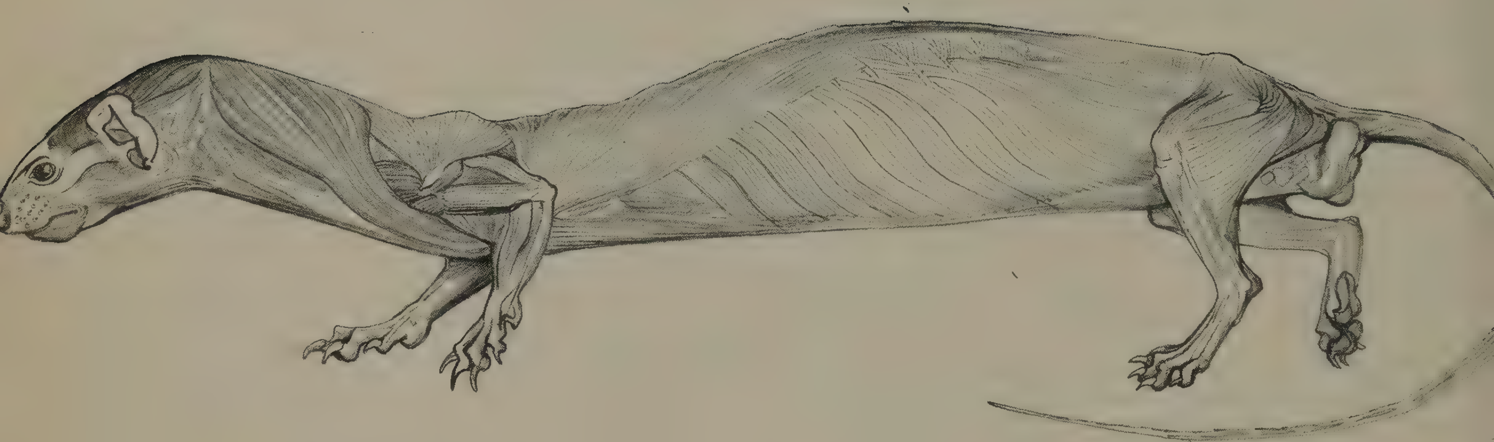
These are the only rodent groups that flourish in any numbers in, or rather under, open pasture or rangeland. The majority of rats and mice need thicker vegetation both as food and refuge. Astonishingly high densities of rodents build up particularly in thick secondary growth on forest margins or in clearings and along drainage lines in moist and montane areas (see Vol. II, pp. 366, 367). *Poecilogale* are less likely to be seen in such habitats but questionnaires have revealed that the striped weasel is well known throughout the areas with a well-distributed rainfall and I think the prevalence of reports from open highland areas is simply due to the weasel's being more visible and that it is only common in areas with dense populations of small rodents that are present throughout the year.

The area from which I have received most reports is the Highlands of western Uganda, where weasels are found in country ranging from forest to the relatively open grasslands of Ankole; in the latter biotope they often live in termitaries. Fallow land after cultivation and the fringes of forest and marsh nearly always support large numbers of rats and mice and in Toro, Ankole and Kigezi weasels are reported to be frequent in such places.

The reason why they are so seldom seen may be due to their activity pattern. Although they are sometimes sighted during the day, perhaps sunbathing outside a hole, Rowe-Rowe (1972) has shown that they are truly nocturnal. Furthermore, their activity centres on a hole which they are capable of digging for themselves very quickly, or which may be a modified rodent burrow or termitary that they have taken over. This refuge is only vacated for hunting and once captured, prey is never eaten on the spot but always carried home and hoarded. This habit has been observed by all who have kept the animal as a pet but an apt illustration of its importance is Rowe-Rowe's description (1972) of two captives given a large fowl, which they dragged together as far as their sleeping box. As they could not get the fowl through the entrance they ate the bird with their bodies inside the box and only their heads protruding. Under natural conditions the burrow is of variable length but ends in a rounded chamber, in which the prey is hoarded. Whenever the weasels have the opportunity, they kill as many rats as they can in quick succession and then take them back. They never tease or worry prey and once it is immobile or just weak and unco-ordinated it is no longer bitten. A healthy rat that lived in the sleeping box of Rowe-Rowe's two captives was not molested for three days, which sounds odd but may suggest that the presence of a rat in the chamber elicits quite different responses from one outside. This observation is interesting because pet weasels have been seen to store living mice after biting the back of their necks and rendering them immobile. Mice have been known to remain in the chamber for three days before being eaten. It is interesting that the related polecat, *Putorius*, is also known to paralyse frogs by biting the spinal chord and then store them.

Weasels have a large capacity and one animal will eat three or four rats in a night. Captives are selective about which parts of the body they eat and they commonly leave the head, tail, legs and dorsal skin of larger rodents.

Although rodents are its main diet it occasionally raids chicken yards and also eats birds. Well-fed captives refuse insects, reptiles, snails, fruit and even eggs and reports of weasels eating such prey may be due to the absence of preferred foods.



Prey is normally tracked by scent but it has been reported that a weasel will open the tunnel of a blesmol and sit and wait. Blesmols usually hasten to repair holes in their tunnel system and it is possible that the weasel takes advantage of this habit.

When it is hunting, a weasel's vision comes into play only at the last minute; Rowe-Rowe (1972) estimated this happened at less than 50 cm. This does not apply to other aspects of the animal's relationship with its environment and Ansell (1960c) thought that his pet weasel used its eyes a lot and certainly chased him by sight. They climb readily and with rapidity.

The bases of trees and termitaries or, in captivity, a vertical surface in the run, are used as defaecation posts. The weasel backs up and, raising its tail, deposits its dung against the surface. Only one or two spots are used for excretion, which usually takes place during the day, so these deposits are likely to be close to the home burrow, which is therefore well-marked, a fact that may have some significance both for the orientation of the owners and for interactions with other weasels. The vertical tail posture is also used whenever the animal encounters an interesting scent (Ansell, 1960c) and its hairs fan out in excitement, whereas the tail is normally relaxed and horizontal. They can be quite fearless and Rowe-Rowe (1972) described a weasel approaching him while he was working in its enclosure.

> "It would bound forward on stiff legs, bouncing on both front feet at once, giving the motion of a rocking action, ending the charge just short of the intruder."

Threats of this sort may be accompanied by a sort of barking scream and ejection of fluid from the perineal gland. The jet can be squirted up to a metre away. When less excited, the weasel utters a high-pitched growl, and a low growl is the first sign of threat. Rowe-Rowe noted that a male directed an often repeated churr towards a female and he interpreted this as signifying pleasurable excitement. He heard a quiet grunt snort when animals were walking about their pen.

Within its shelter the weasel sleeps curled up in a tight coil, but when sunbathing it may extend the length of its back and belly over the ground in a variety of relaxed postures. On the few occasions I have encountered weasels, they have quickly run down a hole or into cover and except for occasional reports of a display I have been unable to discover other reactions to potential enemies. Fleetwood (personal communication) had the impression that an animal he observed running up a tree was taking refuge and Ansell (1960c) commented that his captive "went to ground whenever possible". Their reactions to birds of prey might be important because olfactory defences are probably ineffective against birds and large owls are numerous in most parts of Africa.

Striped weasels have been seen or collected singly, in pairs and in groups that consist of an adult female and up to three young. When the young accompany the mother they keep very close behind her and several observers have remarked on how snake-like they appear when travelling in this manner.

When several are put together in a cage, they fight without respite and often will kill one another (Rahm and Christiaensen, 1963). Rowe-Rowe (1972) introduced a second female to a caged pair and although she immediately displaced the established female from sleeping with the male in the nest box she died or was killed a few nights later. One female was seen to appease the male by nibbling at his cheeks and repeatedly crawling underneath his belly. Otherwise there is very little grooming activity apart from some cursory self-licking. Rowe-Rowe noticed that those animals which had the opportunity to burrow in soil kept their coat in better condition. He also noted that captives wiped their face on the wire of the cage after feeding and that they never cleaned their face with their paws.

He saw a pair dig burrows together; one taking over the mining as soon as the other started reversing out with an accumulation of soil (see drawing). The burrow would seem to be a most important centre for the weasel but it is not known how frequently holes are used, changed or circulated, nor is the range known. However, the hoarding habit implies a relatively restricted hunting area around any one den.

In Europe, the palaearctic weasel, *Mustela nivalis*, does not use shelters permanently, but in Canada (Criddle, 1947), *M. rixosa* does so. In Russia, weasels have been followed in the snow and they are able to average distances of one to five kilometres (Nasimovich, 1949). In other parts of Europe the hunting range of this species ranges between 1·2 to 3·8 hectares (Southern, 1964). This species might, therefore, provide comparable figures for the investigation of *Poecilogale*.

It is very interesting that this species should flourish best in the more temperate conditions of southern Africa and in some of the cooler highlands of tropical Africa. It co-exists with the zorilla over most of their distribution

but appears to be much scarcer in the areas where their ranges overlap, and questionnaire returns suggest that they may be relatively scarcer in drier and more open habitats.

Their nocturnal habits probably help them to avoid competition with mongooses of the genus *Herpestes* and there are generally many more genets than weasels because of the former's catholic diet. *Poecilogale* are probably only fully competitive in areas where rodents are abundant throughout the year. As rodents are subject to considerable and dramatic population peaks and crashes (see Vol. I, pp. 368, 588, 628) one might expect populations of *Poecilogale* to fluctuate as well. There is no information on this but in a locality in south-western Tanzania that I know well this animal was sighted more frequently by me and by other neighbours in the year following a rodent population peak, when there was also a noticeable increase in the number of snakes and owls in the area.

This species is occasionally trapped or killed visiting chicken houses and the skins may be found among the paraphernalia of village medicine men.

Nothing is known about its breeding habits, but extrapolating from information on small palaearctic mustelids, their gestation should be in the region of six weeks. Eibl—Eibesfeldt (1955) studying the ferret, *Mustela putorius*, reported that courtship in these mustelids is accompanied by much growling and that the sexes may alternately grasp one another's neck and drag their partner around like prey. Ferrets may copulate for up to an hour at a time.

The young soon learn to dig but are slow at learning to kill and are still dependent on the mother even after surpassing her in weight. Rowe-Rowe (1972) saw a female leave a partially immobilized rat, on which a young launched its first attack with a well-directed bite on the back of the head. The young are weaned before they start to kill for themselves.

Ansell's pet died at a little more than one year of a fairly longstanding tuberculosis of the spleen and he remarks that the species does not seem to do well in captivity. Nonetheless, captives or free-ranging pets may help to reveal more about the life history of this peculiar little carnivore.

Ratel, Honey Badger (Mellivora capensis)

Family Mustelidae
Order Carnivora
Local names

Nyegere (Kiswahili), Nyejele (Kizigua), Enyegele (Kinyamwezi), Nhegele (Kisukuma, Kiramba), Inyejele (Kigogo), Nyere (Kirangi), Nthegere (Kikuyu), Nthee ya myatu (Kikamba), Kalambaytu (Kiruq), Ikiherele (Kibondo), Kisele (Kipare), Kisegi (Kitaita), Iselle (Kichagga), Omuterere, Entahurira (Runyankole), Entahurra (Lutoro, Runyoro, Luganda), Ekihula, Lwata (Runyamba), Ekorro, Okori (Madi), Ekori (Ateso), Okir (Lwo), Ekitipa, Ekwarri (Karamojong), Oketdwar (Alur), Ekwarra (Turkana), Okulukutu (Lugbara), Ekyone (Kizanaki), Injuro (Kiha), Isenjero (Isukha), Eshambo (Rukiga), Ebunje (Sebei), Engibwe (Lugisu), Kuptoor mwengon (Elkoni), Chepkoget (Kalenjin), Nkarungurungi (Masai), Ama (Kiliangulu), Foruasang (Samburu), Imbulika (Kinyakyusa), Kimbuli (Kimatengo), Libuli (Kipangwa), Mkuli (Kingindo), Zibuli (Kibende), Kiulu, Usamba (Kibungu), Msamba (Kiwabanda), Kimabu (Kingoni), Nsambo (Kisumbwa), Kiata muzinga, Ntalila (Kihaya)

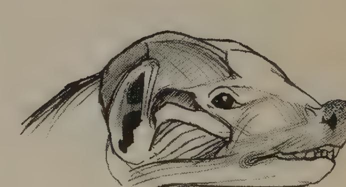
Measurements
head and body
60—77 cm
tail
16—30 cm
weight
8 (7—13) kg

Ratel, Honey Badger (*Mellivora capensis*)

The ratel shares with the zorilla and striped weasel the distinction of being black below and white above. This very conspicuous colouring is correlated with its being virtually free from attack, an immunity it may owe partly to its possession of stink glands but is mainly due to its own physical power and a disposition that veers between fearlessness and unobtrusiveness. In spite of being a relatively small animal it is extraordinarily muscular and its skull is composed of very thick compact bone virtually without sutures. As in all mustelids, the very large cranium is roofed over by temporal muscles. The teeth are robust but are relatively unspecialized. The neck and shoulders are quite exceptionally well developed, the long flexible forelegs are armed with massive claws and are well muscled along their entire length, an adaptation to digging and excavating. By contrast, the hindlegs are without claws, have less flexibility and less power. The skin is very thick and loose and numerous observers have remarked that dogs' teeth make little impression on it; this thickening is even more striking in the region of the throat where the skin is 6 mm thick. Zorillas also have reinforced skin around the throat and I believe this is a protective shield against injury from conspecifics which are possibly more dangerous than the snakes, biting insects or predators that they are likely to encounter. The pinna of the ear is entirely enclosed within the skin so that there is no external ear; when the ratel is digging, an oblique convergence of the margins closes the openings. Small ears are a mustelid trait but the animal's freedom from predators and a primarily scent-oriented sensory system do not provide an adequate explanation for the loss of the external ear (see Pocock, 1908). On the contrary, the ratel listens carefully, particularly at close quarters, and its earlessness might be equally well an adaptation to avoiding damage when attacked. In fact the attacks to which ratels are most frequently subject are from insects, notably bees, soldier termites and ants. It is interesting that the pangolins, which are also fossorial and have to cope with aggressive social insects, should also be earless. However, in their case the scales might damage external ears.

The ratel's diet is possibly less specialized than that of the other mustelids in the range of foods that have been recorded. These include the young of large mammals, rodents of all sizes, insectivores, birds, reptiles, amphibians, fish, arachnids, insects, fruit, carrion and even quantities of grass have been recovered from one stomach. Notwithstanding this, the contents of bees' nests are a major food at certain times of the year and it is possible that the honey badger's local abundance may be influenced by how numerous bees are. Some authors notably Verheyen (1951) and Sikes (1963) have even suggested that there may be a connection between breeding and honey.

It is interesting to speculate on how the taste for bees, their grubs and honey has evolved, remembering what a difficult objective a bees' nest presents to its would-be attacker. Several carnivores show evidence of seasonal switches in diet and this is certainly true of the ratel, whose attacks on hives can be correlated with the ebb and flow of the honey during the drier months (page 103). During the rains, when honey is less widely



available, some of the ratel's most important foods are dung and wood-boring beetles, their larvae and pupae, ants and termites, ground-dwelling rodents and their young, lizards, snakes and tortoises. Most of these foods need digging out and the ratel is functionally adapted to this activity in a primary sense. The relative importance of the foods listed above tends to vary regionally. In cattle country the Masai, Karamojong and Bahima all report that ratels regularly visit the manyattas and dunghills to dig for larvae and in elephant-dominated Tsavo they excavate innumerable holes for dung beetle larvae; vertical shafts dug above the caches betray an uncanny accuracy in locating the larvae (Coe, personal communication). In stony or marshy country, tortoises and terrapins may be locally abundant and favoured foods.

Mellivora capensis

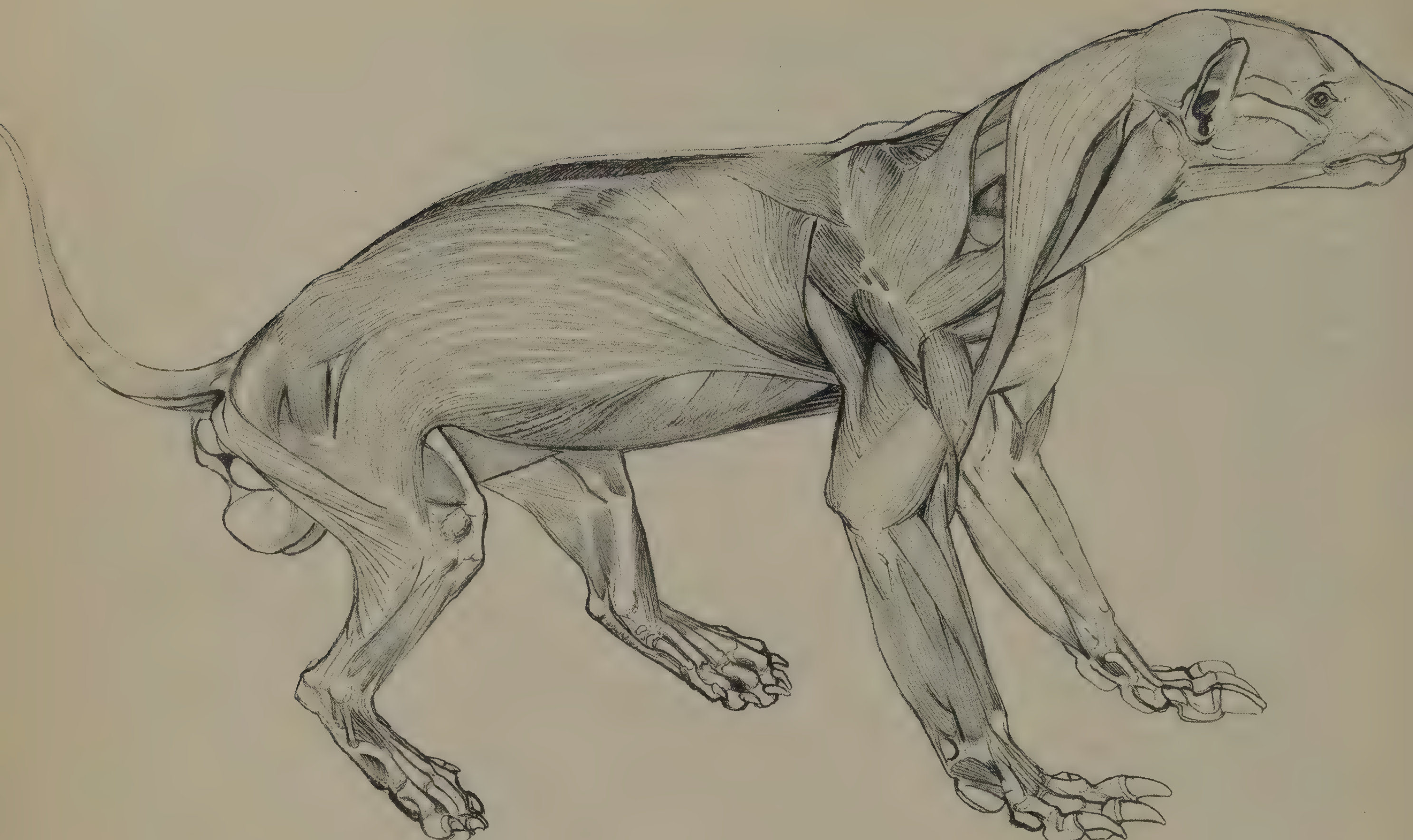
Likewise, breeding rodents are particularly common during the rains in many localities. The prevalence of termite-eating is very largely masked by the activities of *Orycteropus*, whose excavations are similar to those of the ratel. The ratel is almost as able a digger but it seems to be the nests of colonial insects rather than adult swarms that are the main attraction. This is not to say that the ratel does not eat the adult insects, for its dung is often made up of the remains of thousands of bees or termites. But the nest provides a concentration of eggs, larvae, pupae and adults though it is usually well hidden and protected by its situation and by an aggressive caste of soldiers or workers insects. Termites and other social insects are ubiquitous and I think their nests have provided a widespread resource which the ratel has come to exploit by breaking through all the insects' defences. The way in which it neutralizes these defences is one of the most interesting of animal adaptations and it illustrates why a mustelid should have had special qualifications to occupy this niche. It should first be noted that in spite of its thick skin, lack of external ears and coarse, long, hog-like hair the ratel is not impervious to the bites or stings of soldiers and it may roll about or rub vigorously to remove them. In the course of this rolling about, the ratel emits secretions from its gland. Pocock (1920) noted that the ratel's anal pouch was unusual among mustelids in being reversible, as it is in some mongooses and hyaenas, but was unable to give a functional explanation. The ratel, like the hyaenas, extrudes its anal gland whenever it is excited and its glandular emissions are particularly associated with the excitement of finding a hidden nest. The situations in which a ratel uses its anal glands are sufficiently diverse to make it difficult to believe that the secretion always carries the same message, but in the case of exploring and excavating a bees' nest or termitary the effects are unambiguous. I can confirm Pocock's description (1908) of the smell as "suffocating" and this is literally true for the bees, which either flee or become moribund when a ratel uses its secretion, which clearly serves the same purpose as the honey-hunters' smoke fumes.

The following accounts illustrate the ratel's behaviour at a hive:

> "I was herding cattle at Loidim, near Rom, during the first rains (March) when I found a bees' nest in the early stage. I returned later with some other boys to find a ratel there at the hollow tree. The ratel chased us off, so we watched from some nearby rocks and saw it put its anus to the hollow, swirl its tail and then rub its anus all around. The bees were all chased away and then by biting and clawing the tree the ratel was able to scoop out the comb and eat the honey. We saw later that many of the bees had died." (Lokwang personal communication)

> "One night I found one trying to open one of our beehives hanging from a baobab tree. I hurried home to inform father that our hive was being attacked. We hurried back to the hive to find the animal still struggling to open the hive in vain. There was a very sharp smell all over the place. When the hive was lowered, it was found that the bees were gathered in one corner of the hive and that they were inactive, so we did not use the fire that is always used to keep bees out of the combs of honey." (Anonymous correspondent, Manyoni)

I have seen an excited captive make a hand-stand against the wall of its pen and release scent. At the time it seemed an oddly displaced activity but subsequent enquiry suggested it was really quite normal behaviour for a ratel.



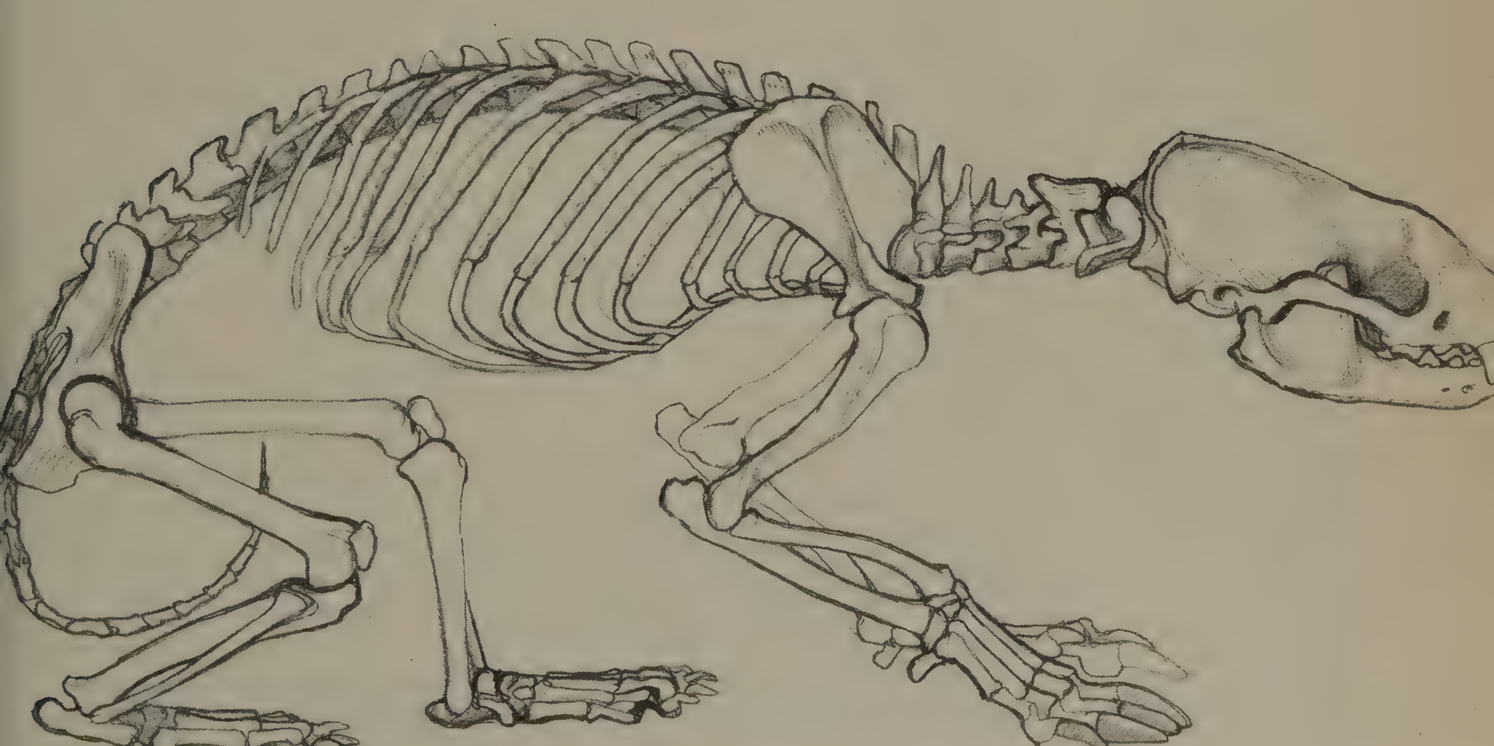
Given that the soldier caste can inflict real punishment on any animal that interferes with an insect swarm, the ratel's strategy is obviously of the greatest importance. I was told of several incidents that suggest that the glands may occasionally not function. A honey-hunter from Suguda Kwa Mtoro found a ratel that had succumbed to the bites of an army of soldier ants, *Dorylus*. These ferocious insects are known to be eaten by the ratel and the males were a special delicacy for Sike's captive. Furthermore three honey-hunters from Kahama and Masasi have reported ratels dead inside their hives and one from Kibondo found one dead nearby, which illustrates how there may be very strong selection for the appropriate behaviour.

Ratels explore any hole or cavity they encounter and there is little doubt that scent plays a major part in finding sources of food, however, Kock (1965) describes a hand-reared captive employing a technique similar to that used by *Orycteropus* (and bears) to explore cavities, in this case man-holes;

> "she would blow down violently, then quickly cock her head to catch the echo with one ear or the other. Having determined that there was a hollow space underneath, she would lift the lid with an expert flick of an accurately inserted front claw."

If wild ratels employ such a technique, they will probably get an audible response from any insects inhabiting a hollow and thus assist the process of finding nests. Because they are numerous and ubiquitous, termitaries probably offer the ratel a year-round source of food not only for the termites themselves but also for the other insects, reptiles, frogs and rodents that shelter therein. In the areas where hollow trees are scarce bees' nests are also commonly found in termitaries but it is stingless species which always nest underground and that are most likely to be encountered by a foraging ratel. Its best clue to the whereabout of arboreal bees' nests is likely to come from the sound of their buzzing. The ratel's hearing is probably acute enough to hear the bees at close quarters but nonetheless it bids fair to miss the majority of hives in an area if it must rely upon its own unaided senses.

In areas where bees are rare, the ratel evidently relies on other foods. For example, Kostin (1963) described steppe turtles and reptiles as the principal foods in Turkmenia. Over most of East Africa, however, bees are a very important seasonal source of food. Fifty-six beekeepers and co-operatives in central, western and southern Tanzania have reported that about 2,700 out of 24,000 hives were damaged by ratels in the course of about one year. Thus, in spite of the keepers' precautions over 10% of the hives are damaged and experienced honey-hunters assert that a much higher percentage of wild nests are found and opened by ratels. This suggests that ratels may be finding more bees' nests than one might expect them to do with their unaided senses. In this they are often assisted by the behaviour of a small bird, *Indicator indicator*, which is very common throughout the wooded savannas. The honeyguide makes itself very conspicuous by calling



Honeyguide
Indicator indicator

repeatedly and displays the white markings on its tail as it swoops in short flights from tree to tree. The ratel follows the bird to a bees' nest, whereupon the bird settles down quietly in a nearby tree. The ratel then casts around, finds the nest and excavates it. The honeyguide only alights after the ratel has left and eats the remaining dead bees, scattered grubs and pieces of honeycomb. (Honeyguides are also attracted to the debris of termites if a termitary has been opened.)

Honey-guiding was first described by Father Jerome Lobo in 1629 but the earliest recorded observation of a ratel following a honeyguide occurs in the notebooks of Atherstone (1953) (in Friedman, 1955). With a distressing lack of detail, Verheyen (1951) summarized his own observation of the behaviour and Friedman (1955) collected some second-hand eye witness accounts and speculated on the origins of the association. In my own efforts to learn something more I have not had the good fortune to see the two animals together but I am well acquainted with *I. indicator* and have followed it to a bees' nest on more than one occasion. I have also watched some of the forest-dwelling species. Most of the African species of the family Indicatoridae are forest birds. One species of honeyguide occurs in northern India but, in spite of congruent distribution having been possible in the past, no association with the Asiatic ratel is known today, nor has guiding behaviour been reported for the bird in India.

The vast majority of African honeyguides collected have eaten honeycomb and even allowing for resistance of wax to digestive breakdown, bees, bee grubs, honey and wax are clearly their usual diet. Of the ten or so species of

honey-eating honeyguides known, only one species habitually solicits human beings. As they are in no way adapted for the task of opening hives they can only rely on mammals or larger birds for assistance. Baboons, chimpanzees, monkeys and squirrels may also attack bees' nests occasionally but the ratel remains the strongest candidate for an original association and his eye-catching colouring may be of advantage to this habit. However, Verheyen (1951) saw honeyguides chattering at antelopes, monkeys, mongooses and a pride of lions. Jackson (1938) had his attention drawn to a serval cat and to leopards by the cries of these birds and he suggested that the calling might therefore represent simple mobbing of potential predators. This is a possible origin for the behaviour but I think the bird's behaviour is probably directed primarily towards other honeyguides and is fairly readily modified into guiding.

I once had the opportunity to watch a honeyguide when it paid almost daily visits to a bees' nest in a tree above my house. My attention was usually attracted to its arrival by chattering and this might be continued for up to twenty minutes. However, it was sometimes to be found sitting quietly outside the nest, its arrival not having been noticed. Unlike the incidents mentioned above this chatter did not appear to be directed at any mammal but gave the impression of being a form of auditory and visual self-advertisement. When calling marked the arrival of the bird at the bees' nest, the chatter subsided after a variable amount of time and the bird would sit sometimes for an hour or more on exposed boughs above the nest and it sometimes hawked after the bees like a drongo. Occasionally there would be spontaneous outburst of chattering again punctuated by silence. Eventually it would fly off chattering as it went, or there might be another outburst some 300 metres away. On one occasion I followed the bird and found it near another bees' nest but I should stress that the bird did not attempt to lead me nor did it show interest in my presence. I think it is possible that these birds circulate regularly around a number of known nests in their home area and this impression has been strengthened on the numerous occasions I have encountered them in open savanna, flying purposefully from tree to tree, sometimes showing little more than an incidental interest in the presence of human beings. Although several birds may converge on an exposed honeycomb, this often gives rise to a chase, suggesting that these primarily solitary birds space themselves out and that they regularly patrol the bees' nests within their area, advertising their presence as they do so. There is probably some overlap of the birds' ranges and Malunde (the chief scout at Makindu) was once led to a bees' nest by a honeyguide only to arrive there simultaneously with a ratel, led by another bird coming from the opposite direction (in Friedman, 1955).

Discussion of this association has tended to suffer from stereotyped or oversimplified ideas about the natural history of honeyguides or honey badgers. A real understanding of the development of this interesting symbiotic relationship would need a much more detailed knowledgeable examination than is possible here, but the following observations may help the inquiry. The honeyguides are brood parasites and they are insectivorous, feeding on a few species of flying and other insects and eating grubs and combs whenever they can find them. At least one species is almost exclusively restricted to the high canopy and other forest species might also be "strati-

fied". *Indicator indicator* is the most widespread savanna species. Unlike some of its relatives, *I. indicator* passes readily from ground level to the tree-tops; in the latter position it is well placed to locate a bees' nest and, during the early rains, flying termite swarms. Both types of insects are captured in flight by means of short forays from a nearby perch, but the bird will alight on the ground and pick up insects around the exits to a subterranean nest. The significance of this bird's association with the ratel lies in its dietary specialization in the same colonial insects. If my impression that the bird makes regular tours around the bees' nests in its area is correct, then the convergence of interests is likely to bring both bird and mammal into regular contact and the mutual profitability of their encounters will soon be learnt, as they come to associate the presence of the other with a rich and concentrated food supply. A mere alertness to one another's presence does not constitute a symbiotic relationship but we have ample evidence that the bird has learnt to solicit both honey-hunters and ratels actively.

As Friedman (1955) points out, if a person does not follow a honeyguide that has apparently come to "lead" him, the bird increases the tempo and excitement of its behaviour as if to urge and entice, or it may just leave and there is considerable variation in their responses.

> "A would-be 'guiding' bird may sometimes follow a person for a very long distance (five miles is the maximum known to me) or for a very considerable period of time (half an hour is the maximum I know of) to attempt to get him to follow it." (Friedman, 1955)

This author goes on to present evidence of the ratel's positive response to the bird. In Nyasaland (now Malawi) he was told by the Chief Justice Sir Robert Tredgold, who was a keen naturalist, that

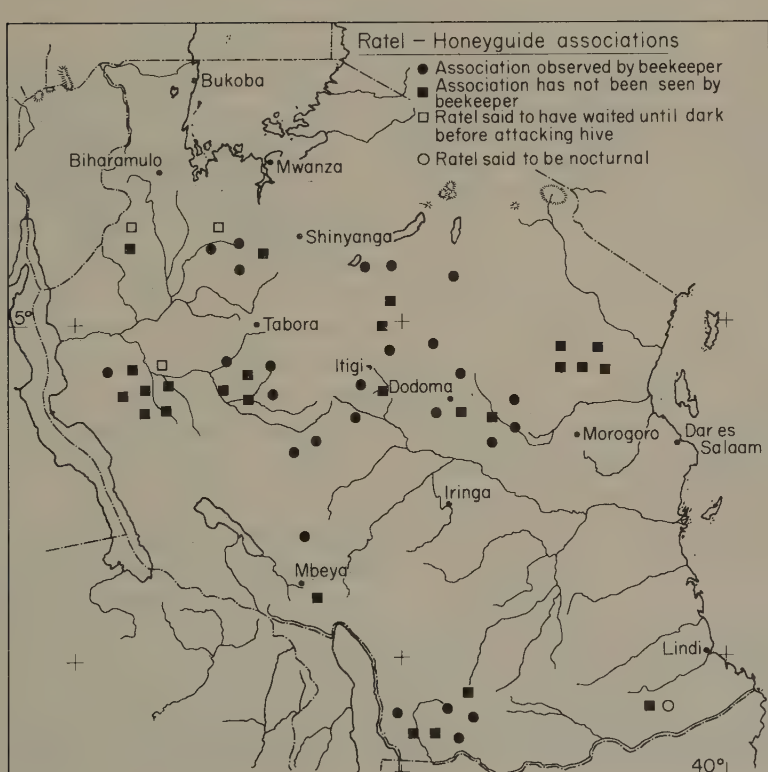
> "he was out in the bush at about 10 a.m. when he heard a grunting, growling sound and also the familiar chatter of a greater honeyguide. As he stopped and listened it came closer and closer until finally he saw an adult *Indicator indicator* definitely leading a ratel, which kept responding with a guttural growl every time the bird gave its chatter call."

Several of my beekeeper informants also describe the ratel answering the bird's cries with grunts.

Having once established a rewarding relationship with the birds, it is not difficult to imagine that a ratel should seek them out but it is still uncertain, and perhaps unlikely, that the ratel actively calls up the bird in the same way that honey-hunters do. There is no certainty that the bird's positive response to being whistled at by honey-hunters relates directly to an expectation of honey, but it could be argued that the mere fact that the hunters' whistle stimulates the bird to investigate and so set off the chain of events leading to the honey could equally be learnt by the ratel, which would only have to grunt more frequently than would normally be the case.

The majority of my informants have made no reference to the ratel answering the bird, saying that it follows along the bird's flight path by listening to the continuous chatter. One beekeeper who claimed to have seen the association frequently said that the ratel only stopped and looked up

when the bird fell silent and that this signified that the bird had reached a beehive. The ratel would then start smelling around the tree and find the nest. Other beekeepers have said that the bird made more, rather than less, noise when it arrived at the nest. My own observation of honeyguides is not conclusive on this point but there is little doubt that the vicinity of a hive marks a change in the bird's behaviour and that it halts its movement. The ratel's responses vary; in uninhabited areas with numerous bees' nests and honeyguides (mainly the tse-tse ridden miombo woodlands, see Vol. I, pp. 32—33) the association appears to be a matter of course and it is here that the ratel is a common member of the mammalian community. It is also more frequently diurnal and this activity might be directly linked with its association with the honeyguide, for it is apparently wholly nocturnal in some areas that have a large human population. Beekeepers in well populated localities are usually familiar with both animals, but their activities are regarded as quite separate. I was therefore very interested to hear of ratels being observed following birds during the day but waiting until dark before attacking the hive. The four independent reports are from three localities in which accelerated growth in the human population has led to a widespread expansion into previously unsettled land (see map). Friedman (1955) quoted Dutton's dawn encounter with a honeyguide leading a ratel in an inhabited locality:



"While being led the ratel was extremely cautious and moved very slowly. The bird was very patient with him and not the usual impatient, vociferous creature it ordinarily is."

The association was then disrupted by a human passer-by.

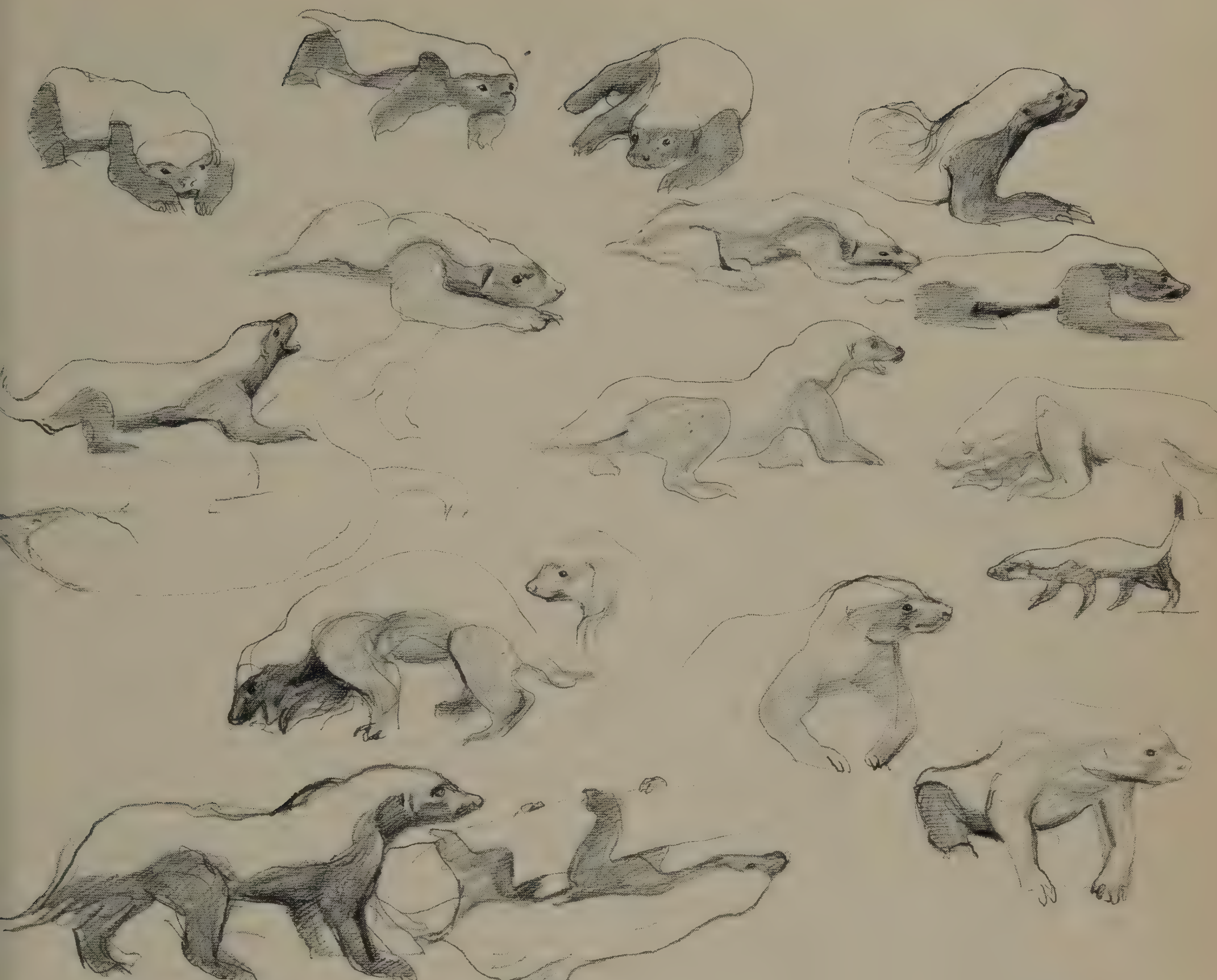
The link between the two honey seekers is evidently a very fragile one and J. G. Williams (in Friedman, 1955) has suggested that guiding of humans is very much less widespread than it was in the past and he fears that guiding may eventually disappear entirely. Could a decline in the guiding of humans be linked with the changeover of the ratel to nocturnal habits and the loss thereby of the bird's most productive partner? And would humans alone supplement the bird's diet sufficiently to reinforce the behaviour pattern?

On the evidence available to date, guiding appears to be a very interesting example of a relationship that probably needs to be learnt by both ratel and honeyguide. Guiding is an example of a little known behavioural phenomenon which is still open to investigation, but it is an opportunity that may disappear before very long. Guiding certainly deserves more attention than it has received to date for it implies the learning and development of a relationship between two very different animals but it also implies a very considerable extension of their food supplies and guiding might therefore influence the ecological success of both species.

Verheyen (1951) describes the honey badger as being exceedingly greedy for honey and honeycomb, probably meaning that the animal's capacity is very large. He also saw a replete honey badger bring several pieces of comb out of the hive. Zukowsky (1924) reports an incident in which a camper took honeycomb from a ratel that he met near Etosha Pan; the animal followed him back to the camp growling and fought with his dogs!

A scattering of honeycombs has been interpreted in honey badger mythology as a deliberate contribution for the honeyguide. However, the enlargement made to the bees' nest usually allows the bird to get in and pick up grubs, beeswax and moribund bees and if the hive is manmade, the ratel will normally have made considerable efforts to get it down to the ground first where it is torn open. If the hive is suspended, it may chew through the ropes, or if it is of the heavy hollow log variety and is wedged in the branches, it may use its back and nape to displace it and heave it to the ground. (Captives spend a lot of their time playing with large heavy objects and getting under them and heaving them about and even juggling them on their backs. One captive was reported always to throw a somersault in the corner of its cage; perhaps in the absence of a plaything the contact of its back with the ground was a substitute exercise.)

Three beekeepers have reported finding ratels killed by falling out of trees with the hive on top of them. This, of course, cannot happen in the areas where the hive is a lightweight cylinder made from *Brachystegia* bark. One beekeeper saw a ratel fell a hive, tumble down and perform its anal ritual and then eat the honey. Taking several surplus combs at a time, it hid them at a distance of some 50 metres and then returned for some more. The ratel is also said to hide chickens it has killed but may not return for them until they have started to rot. An old man remembered watching a



ratel repeatedly removing honeycombs out of a large tree-hole which it had already fumigated with its anal glands. The combs were taken and hidden away beneath a bush. This old man's great-nephew also added that people who have had their chicken houses raided have sometimes recovered bodies buried at some distance from the *tembe* and that a ratel may not return until the chicken has started to rot.

I have several reports of ratels scavenging. The most dramatic incident is described by Cowie (1966), who was watching four half-grown and three subadult lions feeding on a wildebeest they had killed, when three ratels came along and, on scenting the fresh meat changed direction and advanced towards the kill.

"The lions, after some forceful protests and a great deal of snarling and growling, had to give way and wait at some distance until the ratels had finished. With a few grunts and a side glance at the grumbling lions, these curious animals eventually moved off and the lions at once returned to their meal."

A report of two ratels attacking and driving off a striped hyaena at Aruba Dam may be some indication of the familiarity with scavenging these animals have. Smithers (1966b) also mentions ratels scavenging from kills and eating carrion. Monitor lizards and snakes, which commonly shelter in beehives and termitaries, are also eaten and a three-metre python and a cobra have been recorded—the ratel is reputed to be impervious to snake-bite. Smithers also records young and adult kudu being killed, and notes the ratel's power of endurance in running larger prey to exhaustion. In southern Africa they have been recorded killing sheep. I have seven reports specifying that ratels eat bushbuck; one informant in Songea even claimed to have actually seen the ratels actively hunting them. In the Kruger National Park, adult male buffalo, gnu and waterbuck have been found dead from loss of blood after ratels had attacked them in the scrotum.

Independent informants from seven widely separate localities have mentioned the ratel's reputation as a castrator and, although I have yet to come across a man who will admit being a victim, I have met someone who lost his pants to one and lived to laugh it off. One beekeeper from Dodoma went to rescue his hive from three ratels and was able to spear all of them only after beating off their attacks on his "lower parts". He remarked that they only died after being hit "very hard for a long time." The Masai are particularly familiar with ratels which come to forage for the dung beetle larvae in their cattle bomas and the trouserless warriors do not molest the animals, recognizing their own peculiar vulnerability in this respect. It is logical that an animal with more aggression than inches should attack what it can reach.

After the violent and ferocious struggles that ratels often indulge in to get at their food, it is extraordinary what dainty feeders they are. Grubs are extracted individually with the incisors from combs or cocoons that are held meanwhile between the claws; small animals are often skinned carefully and only the softer parts eaten, leaving head and skin. On sheep runs they have been noted plucking out the tongue, eyes and brain of the sheep and eviscerating them through a hole, a treatment of the carcass that is peculiar to the ratel. Adamson (1969) found a puff-adder that had been killed by a ratel biting it behind the head; it had been opened up and only the entrails eaten. These techniques seem to represent extensions of the ratel's expertise at peeling away the various layers that surround its choicest foods, whether these are the wood in which larvae, bees, beetles and termites are hidden, the hardened earth of termitaries or dung beetle larvae caches, the walls of chicken houses, the clay capsules of aestivating lungfish, the waxen or papery cases of insect pupae or the enclosing skin, carapace or bone of animal organs.

Feeding and extraction techniques reappear in a non-functional form in play. Sikes (1963) remarks:

"A tame ratel will carry out manual experiments for hours. If given a wooden box with holes in it, the ratel will study how to drop pebbles into the box and then how to get them out again."

It is just possible that food hoarding provides the basis for the spontaneous dog-like retrieving reported by Kock (1965) for a captive. If captive ratels give any indication of activity patterns, wild individuals may alternate long periods of play, trotting and eating with relatively short periods of rest or sleep, irrespective of whether it is day or night. Even very tame captives resent disturbance when resting (Sikes, 1963) and may respond to the intrusion of strange people, sights or sounds in a variety of ways. Thus Kock's captive first cried in distress at passing buses but later flew at them, trying to bite the tyres. My own captive would threaten ferociously one moment and then retire cringing into a barrel, where it curled up completely immobile. When wounded, the ratel may play "possum" and feign death until its persecutor departs (Bourlière, 1955). In general, it can probably be asserted that ratels are shy (certainly the majority of people have never seen them) but in certain circumstances they may be extremely aggressive and fearless.

The ratel's normal gait is a slow, rather bow-legged lumber, and a clumsy gallop that is seldom seen unless the animal is being pursued by a car. The tail is often raised above the level of the back if the animal is excited. They swim very well and will chase after turtles under water. They can also climb well, although they seem to rely on their own toughness when descending trees or rocks by just tumbling down.

Seasonal changes of diet have been mentioned and it is possible that there may be other changes in the ratel's activity. Verheyen (1951) described it sheltering underground during the dry season but being content with a bush, tussock or fallen tree to rest under during the rains. Several observers, including myself, have seen them active in the midst of very heavy rain. They shelter in rocky caves, amongst tree-roots, in aardvark holes, in excavated termitaries and have even been found lying up inside a wooden beehive. Evidence of the animal's refuge may be manifested by the colour of its coat and I have heard of observers being puzzled by the sight of a brown and pink ratel accompanying a purely black and white one: one explanation could be that the animals had sheltered separately.

Ratels are generally solitary or go about in pairs. The questioning of forty observers as to the largest numbers of ratels seen together at one time resulted in one seeing twelve—seen together in a Masai cattle boma, seeking beetle larvae. Another from the south of the Masai steppe replied he had seen eight and two other observers noted four and six, while 23 beekeepers said they had never seen more than two together and seven had only seen single individuals. One might tend to assume that the pairs consist of male and female but this is by no means certain, for at least one pair caught side by side comprised two adult females.

Given its unusually catholic tastes in diet and habitat, one might expect ratels to be more numerous than they are. Instead it would seem that single ratels tend to be well spaced out, although they might wander very widely. Pitman (1935) stated that they follow definite tracks but gave no details. Despite the trapping and destruction of seven ratels in just over one year, Marks (personal communication) continued to suffer attacks on his hives. Verheyen (1951) asserted that the males are territorial and do not tolerate the presence of other males but he gave no supporting evidence and may have been extrapolating from their generally aggressive behaviour.

As in all mustelids, scent-marking is of the very greatest importance. I described earlier a wild ratel's anal marking as it explored the buttress roots of a tree and fallen branches, and regular marking of surroundings, particularly crevices and holes has been widely recorded. For instance, Hoesch (1964) saw a captive indulge in scenting every time its box was turned around or moved. As is not the case with other mustelids and mongooses, its dung

and urine are not placed on elevated or conspicuous sites but tend to be dropped into crevices or holes, and the ratel may deliberately defaecate into a hole of its own digging. Such sites are more, rather than less, likely to be explored by another ratel; thus dung and urine may be as much a part of the

deliberate marking-out of the home range as it is in otters or in mongooses, which use what are apparently more conspicuous places. Once again there is the implication that the ratel's specialization as an excavator and explorer of holes and crevices is correlated with small but significant alterations in behaviour.

Their social life is totally unknown, but anal secretions undoubtedly have significance here too, for, Sikes (1963) remarks that she was generously pasted whenever she cuddled her pet ratel or whenever it chose to seek contact with her or some other animal companion. The scent message produced in such circumstances must surely differ fundamentally from that made in a state of excited aggression. I had a recently-captured male indulge in what appeared to be displaced anal marking while in a state of great excitement. Fear and aggression alternating rapidly, he would back up to the side of his cage and, making a handstand, paste the door post nearly a metre above the ground on which he stood, swirling his tail as he did so. The rattling roar of an angry ratel is obviously very successfully designed to be intimidating. Sikes (1963) reckoned that the tongue modulated the normal rasping noise, resulting in a variety of calls at different frequencies and pitch; her captive made sharp barks which she interpreted as a desire to go out and whines which were associated with the female's resting periods.

I am not aware of observations on the mating behaviour, but Ewer notes mating in South Africa to occur in February, June and December. Gestation is said to be about six months and one to four young are born in a leaf- or grass-lined chamber. Kostin (1963) records seasonal breeding in Turkmenia with mating in autumn and births in spring. Verheyen (1951) took the word of his trappers that births occurred during the rains and that the animal's greed for honey coincided with the birth season. Sikes (1963) quoted, instead, a Nigerian belief that ratels only mate after feeding on honey. The young probably remain close to the home burrow for a long time. Sightings of adults with small young are very scarce and a female seen at night carrying a cub in her mouth was considered sufficiently unusual to merit mention in a Game Department annual report (T.G.R., 1946). Two beekeepers from Kahama saw some young sun-bathing alone on the sides of a termitary at about 8 a.m. They disappeared down the hole when they saw the intruders.

Young ones are reported to have a plaintive whine and make a hiccoughing cry of distress. It is possible that a slow rate of development is linked with late emergence from the burrow. Hoesch (1964) noted that sight and hearing were still limited in a captive of six months, but this may have been an unusual individual.

The back of a ratel darkens with age but almost entirely black ratels from the humid forests of eastern Zaire are probably local morphs; likewise, a white-headed type has been described from West Africa; albinos have also been recorded. Zoo specimens have lived for nearly 24 years.

I have already suggested how intraspecific intolerance might be the principal controlling factor over density and population dispersal. Diseases might help to reinforce a space distribution and the species is known to suffer from common canine distemper (A. Root, personal communication). Srivastava (1964) recorded the helminths, *Strongyloides akbari* and *Artyfechinostornum*, in an Indian ratel. Beekeepers were unable to account for

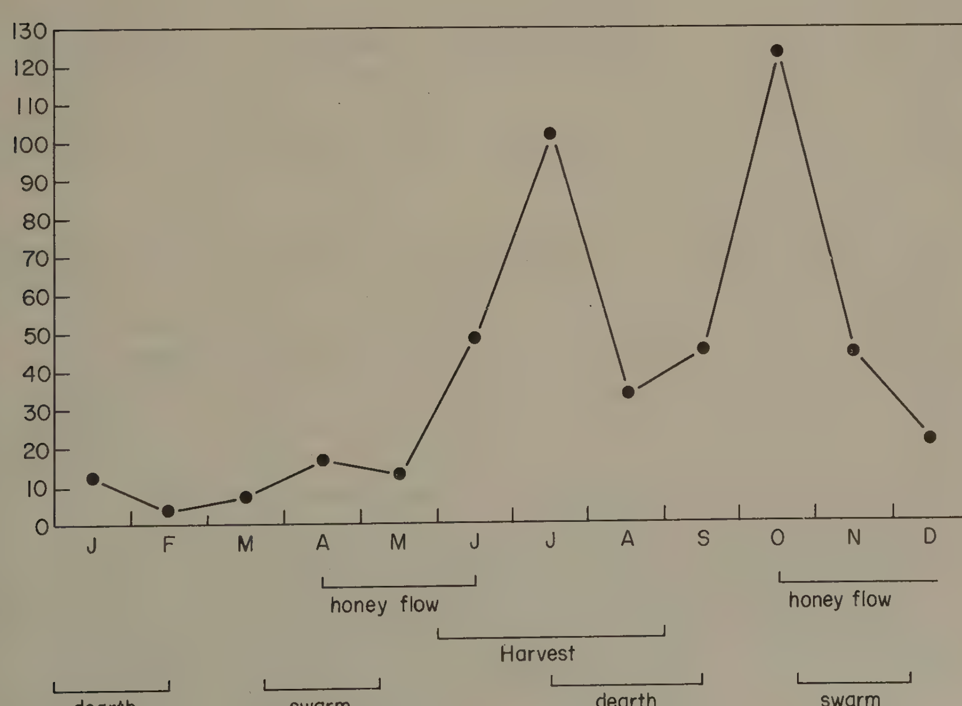
the death of ratels found dead in the bush while another found one killed by a lion.

This species faces an increasingly hostile confrontation from man. The old fashioned honey-hunter seems to have a fatalistic attitude to the ratel's predations and a grudging respect for its intelligence and pluck. In fact, in parts of East Africa, a small boy who fights a bigger one or a man who argues against all odds is sometimes called a real honey badger. However, modern apiculture is less prepared to lose 10% or more of its production to these animals and poisoning, trapping, snaring, shooting and spearing are resorted to with increasing frequency.

Hives hung in trees with a thornbush barrier at the base are less frequently attacked and one beekeeper near Tabora had 156 hives without ever losing one to a ratel so that effective protection is evidently possible. The senior field officer of the Tanzania beekeeping section has written:

> "It would appear that the honey badger will launch attacks on hives of bees at any time of the year with a peak during July–October. We have used wire stands with satisfactory results and I have designed a kind of ground stand which seems to prove satisfactory too." (G. Ntenga personal communication)

I am indebted to Mr Ntenga for circulating and handing questionnaires to beekeepers. His researches in designing deterrents against ratels provide an enlightened contrast to the extermination policies that have been general in southern Africa. Contemporary chemical compounds might reinforce this approach and thus avoid the destruction of large numbers of this extraordinarily interesting animal.



Beehives reported damaged by ratels in central and western Tanzania (1967–68) and beekeeper's calendar

Otters

Lutrinae

Genera and Subgenera

Lutra
Aonyx (*Aonyx*)
Aonyx (*Paraonyx*)

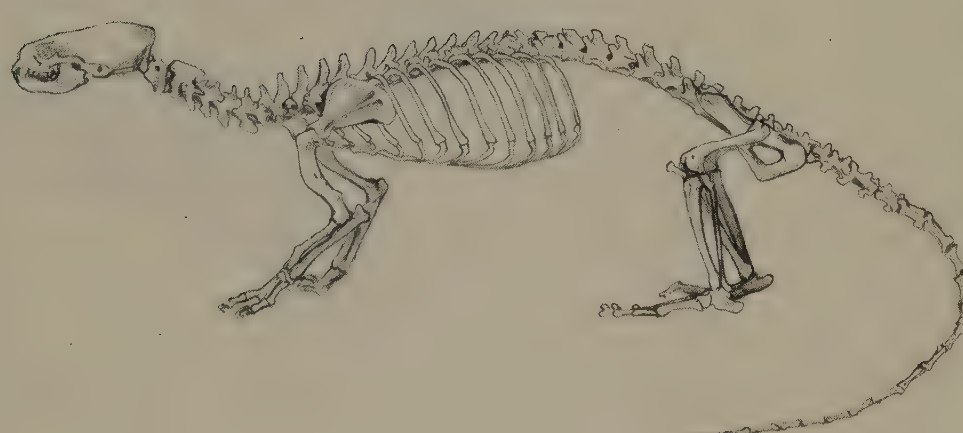
The otters are a group of mustelids which have taken to an amphibious way of life. The incentive for this adaptation is the abundance of animal foods that inhabit inland waters, shores and swamps. Over millions of years this resource has evidently tempted various terrestrial carnivorous animals into the water and whales and seals must be early products of this process. Members of many other mammalian groups have adopted amphibious or semi-amphibious habits. Thus there are water opossums, *Chironectes*, otter shrews, *Potamogale*, (see Vol. II, pp. 11—18) otter rats, *Ichtyomys* and *Hydromys* and *Crossomys*, otter civets, *Cynogale*, not to speak of the marsh mongoose, *Atilax*, crab-eating racoons and foxes and fishing cats. The more aquatic of these species are distinguished by the independent evolution of very dense waterproof fur. Most of them have streamlined bodies and tails to assist swimming or have developed webs between their toes.

Highly specialized adaptations for life in the water are partly the product of time and the most aquatic mammal groups entered the water earliest. In the case of whales and seals a monopoly of animal resources in the sea is shared with predatory fish and sea birds. The only true marine otter is *Enhydra*, which lives by diving for molluscs along the shores of the North Pacific. This species is quite the most specialized member of the subfamily, but it shows some distant affinities with the clawless otters. A distinguishing feature of this group is that they feed on sessile and invertebrate foods and this adaptation is of some significance in any consideration of the otter's evolution and radiation.

The first step into the water taken by a lost ancestral mustelid was probably in pursuit of abundant shore-line animals. An evolutionary shift into a new ecological zone with all the adaptive demands that this entails is unlikely to have been induced by difficult or scarce prey. Although conditions of today may be an inadequate guide, the most abundant and easily caught animals along the margins of swamps, lakes and rivers are snails, bivalves, frogs, crabs, worms and aquatic insects' larvae. Many of these foods are particularly common along sea-shores and it is possible that the ancestral otters combed beaches. However, this was probably a secondary development and the main theatre of action was probably the margins of inland waters.

The African Lutrinae are especially interesting in that they illustrate three quite distinct levels of aquatic adaptation. The tropical lowland forests are traversed by numerous streams and swamps where conditions have probably remained very much the same for many millions of years. As I pointed out in Vol. I, there is evidence for an ecological equilibrium and

stability within the forest biome that has encouraged the survival of numerous animals of known antiquity, so it is interesting to find here an otter that lives upon the very foods that could have provided the incentive for an amphibious way of life. Furthermore, this species has the least specialized dentition of the otters. Rahm and Christiaensen (1963) determined that the swamp otter, *Aonyx* (*Paraonyx*) *congica*, fed upon earthworms, frogs, fresh water crabs and mudfish and they have illustrated a mudbank that had been thoroughly explored for earthworms by the probing fingers of this animal. Around the Kigezi lakes, where the spotted-necked otter, *Lutra maculicollis*, catches *Xenopus* toads in the deep water, the swamp otter inhabits the extensive papyrus beds and seldom ventures into the open water, so although both otters eat a similar food resource there is virtually no spatial overlap, as their hunting grounds and feeding techniques are totally different.



The African clawless otter, *Aonyx*, is clearly closely related and has similar habits to the swamp otter in shallow-water areas. This species is more of a diver, often catching its food by overturning stones and feeling in the sand and mud of the river or lake bottom, but carrying its catches back on to dry land to eat. The activity of searching with the fingers, catching, carrying and finally manipulating the prey while feeding has given this species

extraordinary dexterity. A one-year-old *A. capensis* kept by Maxwell (1960) was still reluctant to go out of its depth and it always disliked going far from land even after learning to dive in deep water.

The fish otters belonging to the genus *Lutra* are more aquatic hunters and the East African representative, *L. maculicollis*, particularly so. This genus actively pursues its prey but still prefers to feed on floor-dwelling fish and crabs and tends to choose the slower or more vulnerable fish species. This genus is scarcely less of a rummager than the clawless species. Maxwell (1960) described *Lutra* fiddling with taps and possessing "an uncanny mechanical sense of how to get things open, a sense indeed of statics and dynamics in general".

Fish otters have the widest distribution of all and occur on all continents except Australia. As a common and highly evolved genus, *Lutra* has been studied more than the other genera and is normally used to typify the subfamily. Some of the adaptations that have received attention are the specialized eyes, which are set very far forward on the skull and are effectively bifocal.

The iris sphincter is exceptionally powerful and can adjust to the shape of the lens by constricting the anterior part (Walls, 1942). In common with some whales and the hippopotamus, the otter's retina is peculiarly ridged by numerous folds in its surface (Pilleri, 1967). Diving requires the ears to be closed and this is achieved by a contraction of the ridges near the base of the pinnae. Ewer (1973) has suggested that diving otters may reduce oxygen extraction by the blood and slow circulation by means of a muscular venous sphincter. As in other aquatic carnivores, the facial vibrissae are exceptionally well developed and have large nerve pads around their roots. A comparison between the three African genera in any of these and other adaptations might reveal interesting graduations in degrees of adaptation to aquatic habits.

Like all mustelids, otters have anal glands, the secretions of which are used for marking objects as well as expelled when excited or under attack. The typically elongated mustelid body and tail would seem to have needed minimal modification for an aquatic life. Clumsy terrestrial humping has been replaced by sinuous undulations in the same plane with extra power provided by the webbed back legs, while the forelegs are reserved for manipulating prey or for sudden changes in direction. The more aquatic the otter the more clumsy it is on land. *Lutra maculicollis*, for example, will always slide down a declivity if it can avoid walking. In fact "slides"—generally dropping into the water—are a feature common to most species and the repeated use of particular routes, landing spots, vantage and resting points encourage the formation of paths. In this way a slide could also be formed, but the slide is a prime manifestation of the exceptionally "playful" nature of otters. Sliding is a game that repeats the first action of hunting, that of slipping into the water; chasing games repeat the hunt, while endless contortions around a food object or its substitute, reproduce the food searching and manipulation phases.

The African otters follow a gradient in the degree to which their prey is aquatic and in the techniques appropriate to their hunting. There is also a linked social gradient. *Paraonyx* is a solitary species (Rahm, 1966) hunting its relatively immobile prey as an individual. Small groups of adult or apparently adult *Aonyx* have been seen together, while *Lutra maculicollis* form large parties and have been seen to attack shoals of fish in what appears to be a co-operative hunt. These groups are discussed in the profile of *L. maculicollis*. The largest social units can probably only form during periods when mothers are not caring for young cubs and when the adult males are not courting, for both tend to be intolerant of other adults at such times.

The most detailed study of otter behaviour and ecology to date has been that of Erlinge (1967a) watching *L. lutra* in Sweden. Single females are centred on the best feeding areas and, in Sweden, they are generally several kilometres apart. It is possible, however, that female dispersal is partly determined by food resources. Adult males are spaced out at even wider intervals and the rapid extension of neighbours' ranges into the territory of a killed otter revealed that the size of a male's territory was probably influenced very strongly by the activity of neighbouring males. Male territories are independent of female ranges but they overlap one or more of them. The males have their own favourite core areas but tend to have traversed their entire territory in the course of several nights and they also pay regular visits

to any female or family core areas within their range. Dung middens and anal glandular secretions are wiped on grass tufts or rocks distributed all over the territory and Erlinge suggests that an autumn peak in territorial activity and scent marking may serve to discourage younger males from setting up their own territories. This author found that the younger animals tended to be transients:

> " the otters seem to behave according to their status in a hierarchic system. Adult dog otters and breeding females are dominant individuals occupying favourable parts of a district. Other otters are subdominant and adapt their haunt and travelling to the habits of the dominants."

Thus evasion and retreat rather than actual conflict are the usual responses between otters, and the territories are maintained primarily by means of threat signals, in which scent-marking presumably plays a crucial part.

The voice may also serve to advertise both the presence and the condition of an otter. All otters seem to use a sort of whistling or chirping contact call. Threats are accompanied by a loud humming or churring noise and if attacked or attacking the otter may scream. Solitary individuals, even of social species may be relatively quiet (see Mortimer, 1963) and it seems likely that there is also a genotypic gradient in this feature with the more social species exhibiting the largest vocabulary. The whistle chirps are capable of many modulations and combinations which communicate a variety of information.

It would seem that not only female otters advertise their reproductive condition. Schreitmüller (1942) described a normally gentle captive male uttering strange sounds over a period of about three weeks during which time he was extremely restless and aggressive and made repeated attempts to escape. Liers (1951) noted belly-dragging as a sign of aggression in *Lutra canadensis*, and he described a captive male making an unusual hooting sound while courting the female. During this period the male scattered his dung indiscriminately instead of using a midden and nipped the female if she approached visitors to their pen. The male takes hold of the caterwauling female by the scruff of the neck when copulating, an activity that takes place on land or in shallow water.

After a gestation of about two months the female gives birth to two to five young in a retreat that may be in the root system of a tree, in some disused burrow or termitary or else in a large hillock of gathered weeds (into which the otter burrows) hidden within the more extensive reedbeds. Any male in the vicinity is driven off before birth and this intolerance of other otters is maintained until the young have learned to swim, some time during their second or third month of life. Rates of development tend to differ from species to species, but they are generally weaned by the time they are five months old and captive females may be sexually mature at one year.

Although otters can be a nuisance to pisciculture, raiding unprotected fishponds or breeding tanks, their predation of fishes in open rivers has tended to be exaggerated by fly fishermen, who assert that angling is fruitless after the passage of an otter. As this phenomenon has been reported to be equally true when the otters are crab-eating *Aonyx* and, as it is essentially a temporary state (Tony Nuti, personal communication), it would seem that

the fish simply do not respond to flies for some time after the otters have passed by. In China and India, instead, fishermen used the otter's ability to scare fish to their own advantage, dropping muzzled otters into the water at selected points to drive fish shoals into large drop nets. Early visitors to Bengal described the children of the local fishermen playing a variety of games with their tethered otters and Maxwell (1961) has given literary immortality to the charms of the otter.

Spot-necked Otter (Lutra maculicollis)

Family Mustelidae
Order Carnivora
Local names
Fisi maji (Kiswahili), Engonge (Luganda, Lutoro, Luhaya and other languages), Engonji (Runyankole), Ngonyi (Lukiga), Anziri meri (Madi), Njimbiri (Kikuyu), Mengib bey (Kalenjin), Ababuse (Ateso)

Measurements
head and body
46—76 cm
tail
40 (30—51) cm
weight
5 (3·5—9) kg males
4 (3—5) kg females

Spot-necked Otter (Lutra maculicollis)

Races

Lutra maculicollis nilotica	Nile, Lake Victoria
Lutra maculicollis tenuis	Kigezi
Lutra maculicollis chobiensis	South-west Tanzania

Lutra maculicollis

This sleek otter can be distinguished from the larger, more heavily built clawless otter by its blotched or spotted neck and belly, a thicker and relatively longer tail and by its more aquatic habits. The hands and feet are clawed and webbed to the tip of the digits.

The distribution of this species is restricted in eastern Africa. In the first place it is totally dependent on water and so does not occur in rivers which dry out seasonally. Furthermore, it seems to be absent from most of the low-lying rivers and lakes, even when these are continually and plentifully stocked with fish, whereas it may be common in small montane streams at higher altitudes which would seem to be poorer in fish. They are common in parts of Lake Victoria, particularly where the coast is rocky and they also occur in Lakes Tanganyika and Nyassa. They are absent from most of the eastern Rift Valley lakes and apparently from many of the East Coast rivers.

Otters kept by Alan Root in an enclosure near the shore of Lake Naivasha have flourished on a diet of Naivasha fish but an important limiting factor for the species as a whole may have been revealed when these adult otters escaped into the lake. They returned with numerous leeches firmly attached to their webs, eyelids and lips and the otters appeared to be unable to remove them. Perhaps the typical exploratory hunting behaviour of this species tends to bring them into contact with leeches, but this should be even more true of *Aonyx*, the clawless otter and the marsh mongoose *Atilax*. In their case, however, greater manipulative abilities might enable them to remove parasites encountered in what are often muddy, leech-ridden habitats. Notwithstanding this, neither otter species occurs naturally in Lake Naivasha in spite of new crustacean and fish resources introduced by man, whereas the marsh mongoose has become exceptionally common, making the most of the Louisiana crayfish that are now so abundant.

The introduction of fish by man in formerly fishless lakes does not necessarily benefit the otter and the case of Lake Bunyoni is an interesting one. This deep, high-altitude lake was one of several in Kigezi and Ruanda where a species of clawed toad was the dominant aquatic form of life. The number of toads was immense, supporting a variety of birds and large populations of two species of otter as well as supplying quantities of protein to the Bakiga. In the 1920s fish were introduced into these lakes and in the netting that followed otters frequently became entangled and, because of a tendency to come to one another's aid, their numbers were soon reduced.

Populations of *L. maculicollis* generally have a thin and scattered distribution. It is interesting, therefore, that the frogs enabled the Ruanda and Kigezi population to become exceptionally large and densely aggregated.

Otters from this area have been treated as a distinct race and even species, *L. tenuis* (Schouteden, 1947). It would have been interesting to compare the biology of these animals with those in other areas but the distinction of density is now lost because the Kigezi otters, although still in existence, are no commoner than in other areas.

Elsewhere frogs are also an important part of the diet but fish are undoubtedly their main food. Procter (1963) noted that *Haplochromis* was the most important food fish in Lake Victoria. These fish are amongst the most numerous small fish in the lake and they are also relatively conspicuous and slow, all major considerations in determining what species and ages of fish are eaten. The otters probably choose conspicuous, slow fish between 10—20 cm in length with occasional kills of up to 60 cm *Bagrus, Barbus, Clarias, Protopterus* and *Tilapia* have been recorded in their diet as well as molluscs, crabs, waterfowl and other birds, their nestlings and eggs, mice and aquatic insects and their larvae. Proctor watched one chewing sedge and Mortimer (1963) had a pet which went into his kitchen garden to eat fresh carrots, beans, peas and potatoes. In some areas they are known to take poultry and eggs from the villages and Rahm (1966) watched a captive carry eggs in its mouth to its shelter. Once there it grasped the unbroken egg between its forepaws and opened it most delicately, extracting the contents without swallowing the shell. The availability of some foods must be strictly seasonal. Parties of otters in Lake Victoria give every appearance of swimming and feeding in a group and social hunting is likely to be more successful than individual searching and chasing. McMaster (in Shortridge, 1934) noticed that schools of otters combining their efforts surround and drive a shoal of fish, a phenomenon that certainly deserves further study. Solitary otters can occasionally be seen floating, with their tail trailing along on the surface and their heads facing straight down under the water; others have been recorded turning over stones on the river bed. If their catch is small or they are at a distance from land, they may float on their back and use their chest as a table, but they normally prefer to land and eat off a rock or bank. The head and backbone of large fishes are sometimes left but most fish are eaten from the tail upwards, mouthfuls being sliced out and bolted with minimal chewing. In spite of their webs the hands are surprisingly adept and are used to handle any food or play-object that is being bitten or mouthed. When the otter is hungry, it eats without preliminaries but as hunger is appeased there is usually much play with the fish before it is eaten.

The process of hunting and catching is protracted by an increasing readiness to lose and then find again a maimed or exhausted fish. The more the otter has eaten the less like food-catching does its activity become and the repeated chases and seizures become progressively more playful.

Like all the otter family, this species spends a great deal of time playing. This activity usually follows the morning's hunt which starts at about dawn and may last about two and a half hours. Procter (1963) watched them haul out on to rocks where they played, groomed and sun-bathed and then retired deep into rock crevices, presumably to sleep. Various activities are typical of these play sessions; twigs, leaves or stones as well as fish remains may be mouthed, nosed, patted or thrown and the body is coiled, twisted, rolled or slid through the water or over the ground in endless contortions around these

play-objects. Sometimes the object of their attention becomes another otter, in which case there is chasing and wrestling. This often subsides, turning from gentle nipping and biting into mutual nibble-grooming or a tight hug. Although they do not lick themselves or one another, they very commonly suck their own front paws or a tuft of belly fur. This very baby-like gesture is often seen in captives of all ages and sexes and while it might derive from sucking it also suggests a satiated otter mouthing or tasting a food or play-object as it passes from its active phase into dozing or sleep during the middle of the day.

The second activity period normally begins at about 4 p.m. and continues till nightfall. Both captives and wild otters have been seen to be active on

moonlit evenings and it is possible that partially nocturnal habits may be adopted in areas where they are actively persecuted. However, the pre-eminence of visual cues in hunting probably discourages entirely nocturnal habits and the moonlight activity is often only an extension of the evening hunt and its successive play.

The tendency to land after feeding ensures that the otter drops its dung on

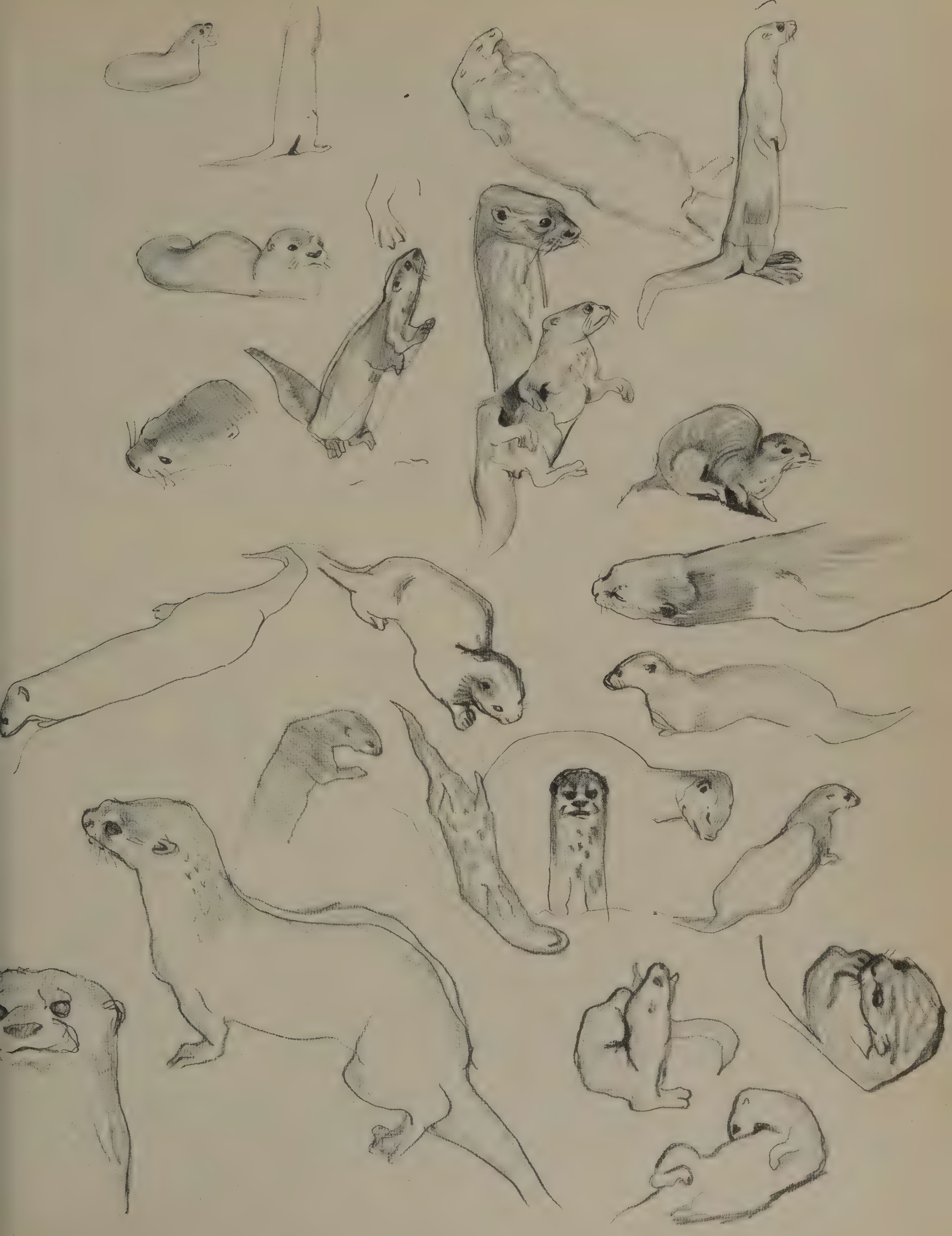
the shore. Digestion is very rapid and captives have been found to excrete the remains of fish eaten one hour earlier. However, dung also plays an important part in their social life and is therefore not wasted in water. Urine is generally deposited in the same place and Procter noted that these otters actually come out of the water in order to urinate on land. The importance of this social activity is betrayed by the striking postural difference between sexes, the male raising his tail vertically while his urine is directed forward, and the female holding her tail horizontal while she urinates backwards.

While running, *L. maculicollis* humps its back much more than *Aonyx* and it also tires quickly if forced to go any distance on land, betraying thereby its total dependence on water. In crossing land the otter may make use of a declivity to slide down on its belly and Mortimer (1963) thought he had found a regularly used "slide" on a dam wall in Zambia. The habit of sliding may be as characteristic of this species as it is of the other one but it may also depend on the physical characteristics of the shore, because Procter did not see the Bukoba otters indulge in sliding, although they did rub themselves on the rocks. He did see them, however, make dives from heights of up to two metres.

In the water the body is propelled by undulating movements, with extra power exerted by a thrust of the webbed hindlegs.

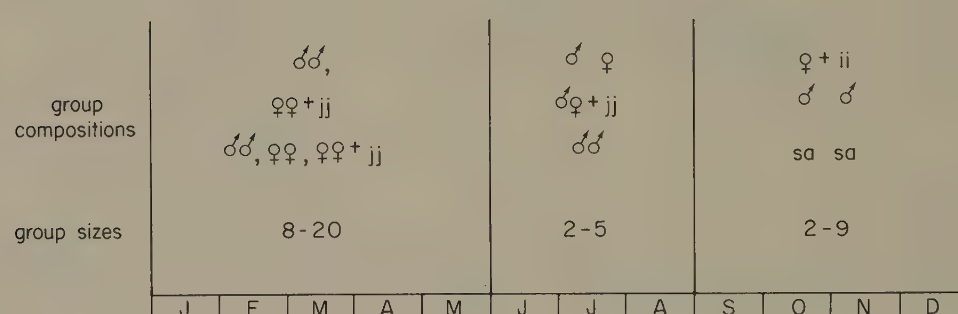
The spot-necked otter is one of the more social species and it is interesting that Mortimer (1963), keeping a solitary animal, should have thought it a relatively quiet animal. Procter watching wild groups in Lake Victoria lists, instead, a variety of distinctive noises among which are the typically lutrine throaty whistle, a short "yang" and a long harsh mewing call. All these sounds may serve as contact and or want calls; the last is typically uttered on land by a lone individual. Mild alarm is expressed by a gasping noise which becomes a spluttering snort at higher intensities. The most commonly heard noise is a rather bird-like chattering. This rises to a shrill trilling noise if one animal is threatened by another and it seems that this noise, particularly if combined with neck stretching or lying on the back, may imply submission. This interpretation is suggested by the behaviour of captive young, which tend to adopt definite hierarchies.

Living as it does in a variety of habitats and at differing densities, the spot-necked otter may have a relatively plastic social life. Observations from Lake Victoria suggest that in this region there might be a regular annual cycle of aggregation and dispersal. Procter (1963) thought formal territories were unlikely at Bukoba where otters are only temporarily resident. However, he noted distinct sexual groupings with the largest schools tending to be aggregations of young or non-breeding males; he also noted that these bachelor groups were more mobile. As annual breeders drive off one litter just before the birth of the next, it is probably the coincidence of this seasonal event that leads the young to gravitate towards others in a similar predicament. Procter thought that the young females formed smaller, less mobile groups, an observation that implies that in this area the otters do not have young until they are two years old. The larger size of the male groups may be due to the addition of mature males, which are also not tolerated by females with young. For three months the mothers remain alone with their new litters and it is possible that the wandering of males is due to exclusion from the



most favourable areas by the lactating females. This intolerance of other otters probably breaks down once the young are fully mobile and begin to eat solid foods and it is perhaps at this stage (February to April) that the largest mixed parties are seen in Lake Victoria.

Procter describes families beginning to move about in January joined by young of the previous year, but an exclusively family-like structure—typically two adults and three young—is apparent by June. It is possible that this development is the result of adult males driving off other mature males and monopolizing a female, and it would be interesting to know whether this actually takes place and whether the males make spatial as well as sexual claims at this time. In Sweden older males of *Lutra lutra* show a



Tentative calendar for otter associations in Lake Victoria: i. infant; j. juvenile; sa. subadult

peak of territorial activity and scent marking in the autumn which, Erlinge (1967) suggests, may serve to discourage the competition of younger males which are also trying to set up territories at this time. It may be that *L. maculicollis* is also territorial between June and August.

Females may have their litters in a variety of places; rock crevices, floating papyrus, small islands and they have been reported climbing up into the roots or hollow branches of riverside trees. Gestation is just over two months. Details of the development of the young have not been recorded, although this species has bred readily in captivity. The young learn to swim when they leave their den at about two months of age and the mother is scarcely ever parted from her young for nearly a year, although females reach adult size by the age of seven months. Learning to fish is a long and slow process and is better known for related species. The mothers are fiercely defensive of their young both against other predators and man; their defences include the emission of anal secretion which, although unpleasant, cannot compare with that of the zorilla.

A major factor in this species' decline in certain areas may have been the introduction of nylon fishing-nets in which an otter, once tangled, drowns, attracting in its struggles others of the party, which in turn get caught. In

Lake Bunyoni, it is uncertain whether nets or the decline of the clawed toads have been primarily responsible for a reduction in their numbers. In the past they had not been greatly affected by the hunting that was an ancient tradition for the shore-dwelling Bakiga,

> "who spent most of their week-ends (in the afternoons) otter-hunting. When eight or a dozen dug-outs co-operate it is a noisy business but rather picturesque. The otter usually escapes. The otter spear is six to seven feet in length with a stout but slender wooden shaft: it is made entirely of wood and the four prongs are set forward and slightly outward (in a square) from the end of the shaft." (U.G.R., 1935)

The fur of these otters is greatly prized and is widely worn as a wristlet and used to wipe infected eyes or nose. It is thought to soothe or cure these infections!

Mortimer (1963) kept one otter of this species and noted its great dependence on water, betraying distress on dry hot walks and seeking water as soon as its eyes or muzzle became dry. Its ability to trace even small quantities of water hidden in flower pots, etc., was particularly striking.

The frequent death of captives suggests that they may be subject to a variety of diseases, particularly when under stress.

Swamp Otter
Aonyx (Paraonyx) congica

Family Mustelidae
Order Carnivora

Measurements
head and body
85 (79—97) cm
tail
50 (41—56) cm
weight
13·6—34 kg

Swamp Otter
Aonyx (Paraonyx) congica

Races

Aonyx (*Paraonyx*) *congica congica* Bwamba (probably)
Aonyx (*Paraonyx*) *congica phillipsi* Kigezi

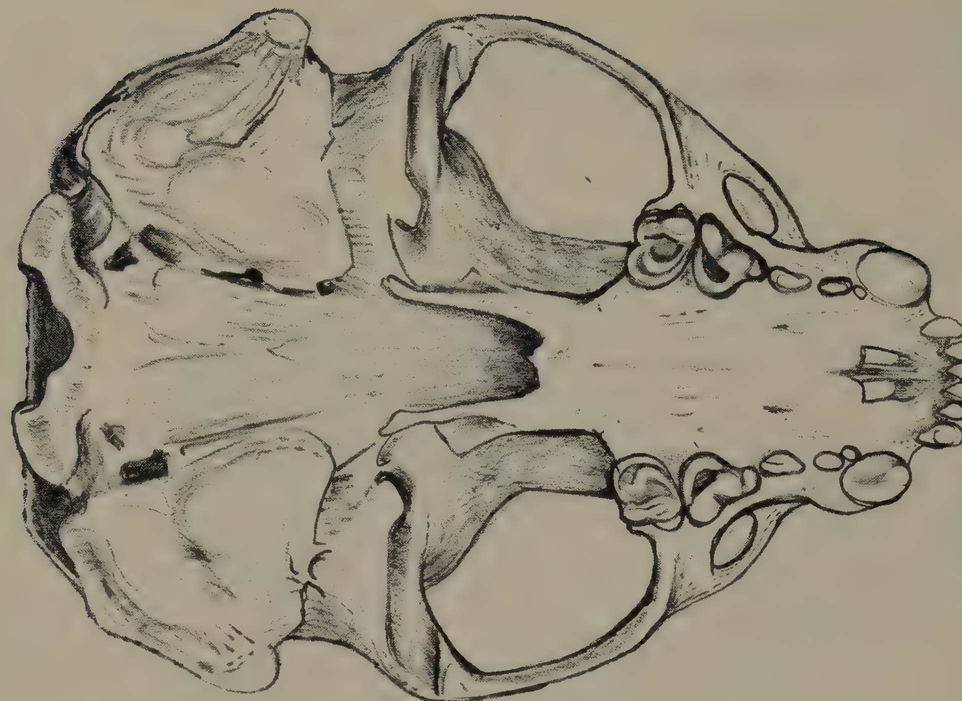
Of all the otters, this animal is the least adapted to an aquatic existence. Its dark fur, although soft, is shorter and thinner than that of the other species, the hindfeet have only developed webs as far as the base of the second phalange, while the unwebbed forefeet are both hairless and clawless. The naked feet and vestigial claws are the most peculiar features of the animal and are adapted to feeling for food in soft soils, debris and mud.

The cheek teeth are well suited to chewing a variety of animal foods and are less specialized than those of *Aonyx* (*Aonyx*). The colouring of both genera is very similar but the head and neck of this species are frosted with silver-tipped hairs and there are conspicuous dark patches between the eyes and the nostrils. The fur of the high altitude Kigezi otters is darker and softer than that of the lowland *A.* (*P.*) *congica congica*, but these are pelage qualities that are common in many mammal populations living on mountains so that the racial distinction may turn out to be invalid.

It was Hinton (1921) who first recognized that this otter was quite distinct from *Aonyx* in spite of uncanny resemblances in colouring and size. He was inclined to regard it as a retrograde or degenerate form, deriving from a *Lutra*-like ancestor. Instead it would seem that *Paraonyx* provides an illustration of the ancestral otter. This is not to suggest that it is directly antecedent to otter genera or species, because the specialization of its limbs and digits, particularly the hands, is advanced.

Within the tropical high rainfall area the microfauna of the swamps has not had to evolve strategies to insulate against periods of drought, as a result both montane marshes and lowland swamp forests tend to have a year-long abundance of worms, insects, molluscs, crustaceans and amphibians and it is this resource that sustains the swamp otter.

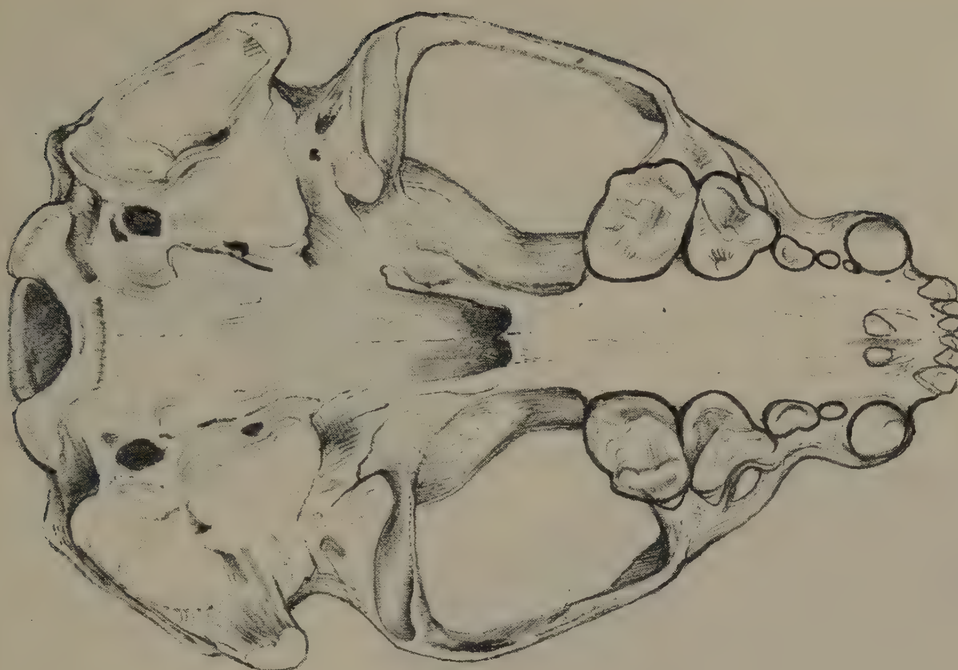
The position of the otter itself within the ancient swamp habitats of the tropical forest zone should be considered. These habitats have both a seasonal and a long-term ecological stability which may itself secure advantages for species that adapted to these conditions at an early date. The most likely competitors for *Paraonyx* are the marsh mongoose, *Atilax*, and the clawless otter, *Aonyx*. While there is a considerable dietary overlap between these three species, *Paraonyx*, secure in the prior occupation of its niche, might be specifically superior at extracting prey hidden in the thick and overgrown muds of the tropical swamps. Also *Atilax* sifts through muddy water but it is lightly built and possibly not dextrous enough to tackle animals such as worms in thick mud and debris. The grotesquely exaggerated teeth of *Aonyx* are an unquestionable advantage when tackling hard carapaces, shells and very bony fish, but prey with such defences does not represent a major food resource in the swamps of the forest zone.



Aonyx (Paraonyx) congica

A. (P.) c. phillipsi was originally described from papyrus swamps on Lake Bunyoni at an altitude of about 2,000 metres; in this lake it shared the formerly very abundant frogs with *L. maculicollis*, and Pitman described the swamp otter as living on crustaceans, molluscs, eggs and young birds as well. Rahm and Christiaensen (1963) described and illustrated the excavations of this animal as it searched out earthworms in mud and soft soils. Rahm (1966) added fish and fresh water crabs to the list of foods and he has described *Paraonyx* as solitary or in pairs and being nocturnal. Robert Glenn (personal communication) has seen this species in the papyrus swamps of Lake Mutanda during the day. In this area, the animal is still known and hunted, despite the widespread drainage of the swamps, and wristlet amulets of its skin are sometimes worn by the Bakiga.

Summarizing the effects of the luxury fur trade, De La Fuente (1972) singles out the pelt of the West African race, *A. c. microdon*, as being in great demand in Europe. It is paradoxical that a fur should be a familiar and greatly valued object of trade and superstition while its owner's habits, behaviour and status are virtually unknown even in the late twentieth century.



Aonyx (Aonyx) capensis

Hands and feet of *Paraonyx*

African Clawless Otter

Aonyx (Aonyx) capensis

Family Mustelidae
Order Carnivora
Local names
Fisi maji (Kiswahili), Engonge (Luganda)

Measurements
head and body
72—91 cm
tail
40—71 cm
weight
20 (18—28) kg males
18 (13—19) kg females

African Clawless Otter
Aonyx (Aonyx) capensis

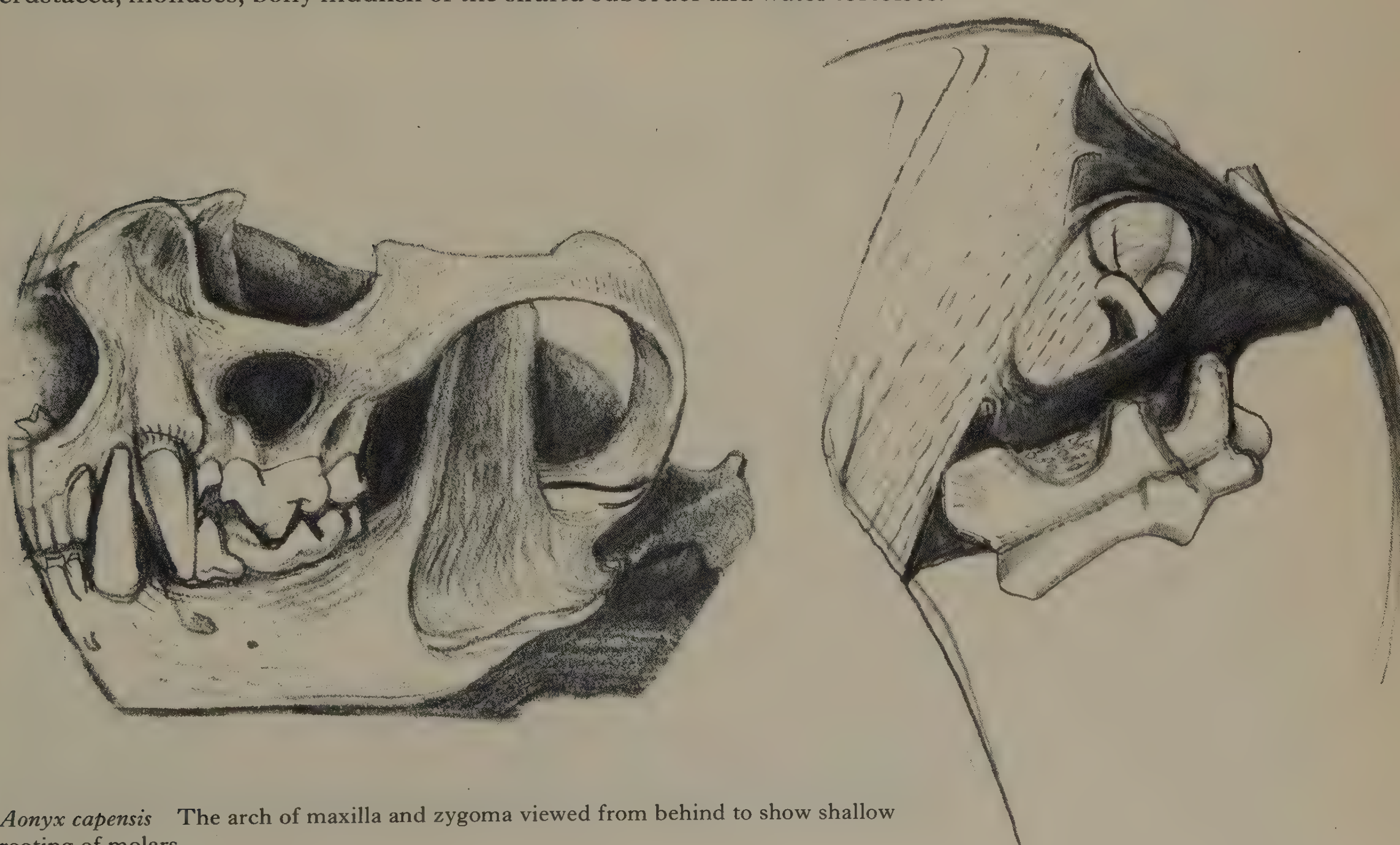
In describing a pet clawless otter, Maxwell (1960) made a string of references to fine fabrics and elegant tailoring, exemplifying thereby the admiration that this animal and its fur excite in people:

> "The bib is divided from a silvery brocade-textured head by a sharp line of demarcation immediately below the ears; the body and the enormous tail are pale mauvish-brown velvet above and silk below. Beyond the points of attachment at the four wrists the fur is of an entirely different character; it changes from velvet to satin, tiny, close-lying hairs that alter colour according to how the light falls on them. The tightly gloved hands and the enormous fullness above the wrists give her the appearance of wearing heavy gauntlets."

Aonyx capensis

These hands have almost webless digits, blunt, finger-like and without claws. The hindlegs are webbed but are also clawless.

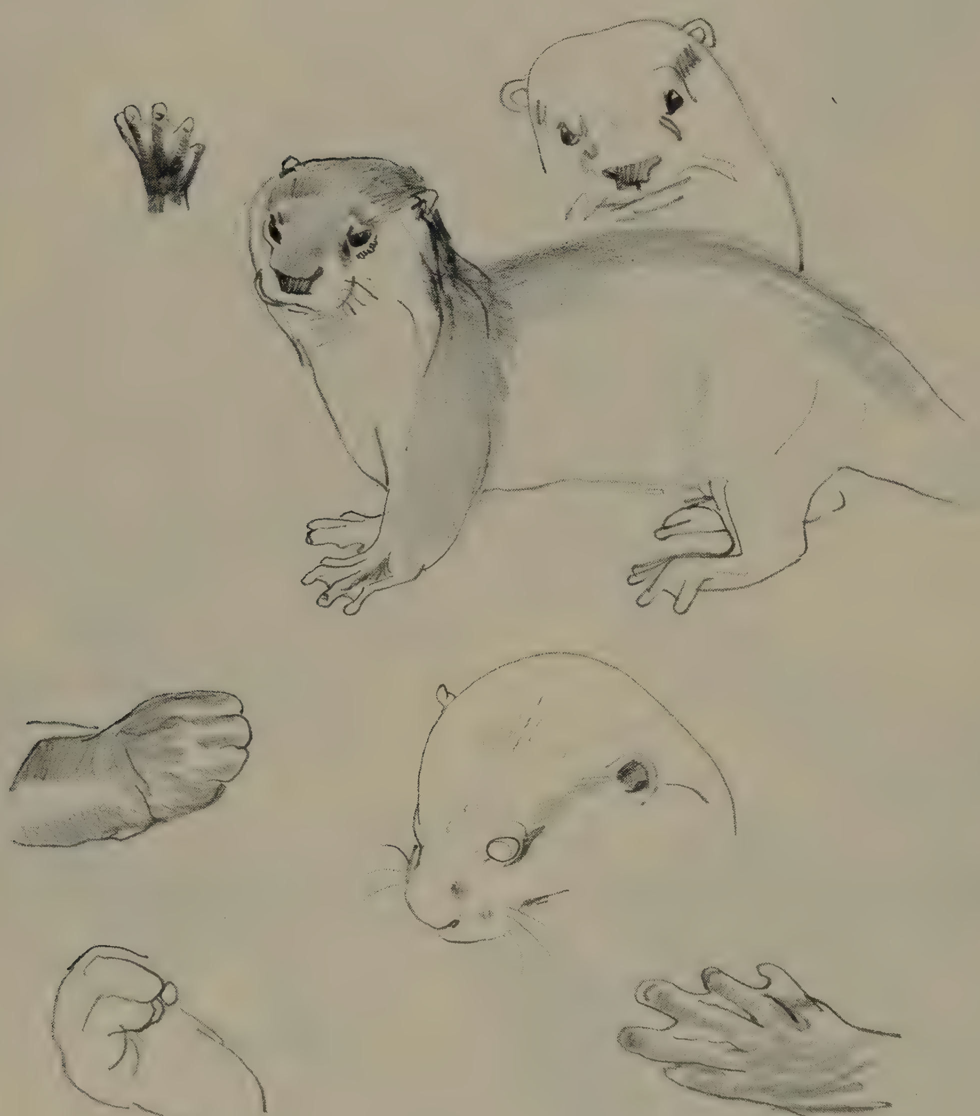
The molar teeth are extremely large and have plate-like surfaces with low, ill-defined cusps. Although the zygoma and the lower mandible are deep and robust, the teeth seem quite disproportionately large for the base of bone out of which they grow. The skull is flat and exceptionally broad across the mastoid region with low but stout occipital and parietal crests. These cranial and dental peculiarities are related to the animal's diet, which is mainly crustacea, molluscs, bony mudfish of the silurid suborder and water tortoises.



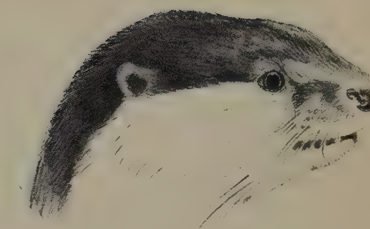
Aonyx capensis The arch of maxilla and zygoma viewed from behind to show shallow rooting of molars

These foods are crushed up whole and the power is mainly exerted by the huge *temporalis* muscles, which are spread over the whole roof of the cranium. In the absence of large ears, the external form of the head is modelled to a striking degree by these muscular masses.

The hands with their mobile fingers and round excrescences (see drawing) are also adapted to this specialized diet, as *Aonyx* exposes its prey by feeling, at which time it averts its head as it churns up the mud or overturns rocks and other debris on the bottom.



This species inhabits swamps, rivers, streams, lakes and estuaries at all altitudes whenever there is enough permanent water to support crabs, molluscs or mudfish. In the main forest block its niche is occupied by *Aonyx* (*Paraonyx*) *congica*.



An important food in most areas is probably the fresh water crab, *Potamonautes*, but in some marshes mussels like *Unio* spp. and large aquatic snails of the genera *Pila* and *Lanistes* may be more common, while in swamps and muddy rivers catfish, *Bagrus* and *Clarias* and mud turtles, *Pelomedusa*, are likely to become important, particularly during the dry season. Many other foods may be taken, especially frogs, various water fowl and their eggs, monitor lizard and crocodile eggs, cane rats and other rodents and I have found the remains of dragonfly larvae in their dung. A clawless otter was seen to take a Peter's finfoot, *Podica senegalensis*, while it was swimming in deep water by seizing it from below by the legs.

Copley (1950) noted these otters eating young maize cobs; although captives show a fondness for some fruits and sweets I never found any trace of seeds in quantities of collected dung, in spite of their riverine habitat being littered with fallen fruit of various sorts. With the exception of the flesh of palm nuts, upon which many carnivorous animals will feed, vegetable foods are likely to be resorted to only *in extremis*.

Because crabs are likely to nip the sensitive fingers, *Aonyx* has a special technique for dealing with them, flipping them over or even out of the water, where they can be more easily bitten. Maxwell (1960) described three ways in which his tame otter threw up objects.

> "The most usual was a quick upward flick of the arm and forepart of the body as she held her clenched fist palm downwards, but she would also perform a quick backwards flick which tossed the object over her shoulder to land at her other side and, on occasion, usually when in a sitting position with her back supported, she would throw overarm."

She also used her tail to sweep objects within reach of her hands.

Food is generally chewed at while held fast in the hands, with the animal resting its weight on the elbow. When food is eaten in the water, which is rarer, it may be chewed while the animal is floating on its back and this lolling attitude may be adopted on land, particularly when the animal is nearly satiated or is playing with a piece of food or other object.

Captives often carry proffered food to the nearest water and dowse it, scrabbling about in the dish and pulling it up again before eating. Likewise, a dead or dying food object may be allowed repeatedly to sink to the bottom of a pool where it will be dived for and refound again and again. This diving and dowsing seems to be the equivalent of wounded fish-chasing in *Lutra* and it is interesting that the play pattern in each case should be based upon their very different food-finding techniques. When an object is carried it is rare for it to be taken in the teeth but it is usually held against the chest.

The walk is rather heavy, with a slight waddle due to the shifting balance of the back but, because this is less elongated than that of *L. maculicollis*, its gallop is less "caterpillar-like" and it is certainly less ungainly on land. Unlike *Lutra*, it hunts very little of its food by sight and touch, smell and hearing play more important parts. Because it does not rely on sight, *Aonyx capensis* can seek food at any time of the day or night. I have seen several in the late afternoon, swimming after one another across the open waters of a crater lake and they are not infrequently seen basking on banks and rocks in the

sunshine, at which time they may fall asleep. However, the greater part of their hunting takes place at night.

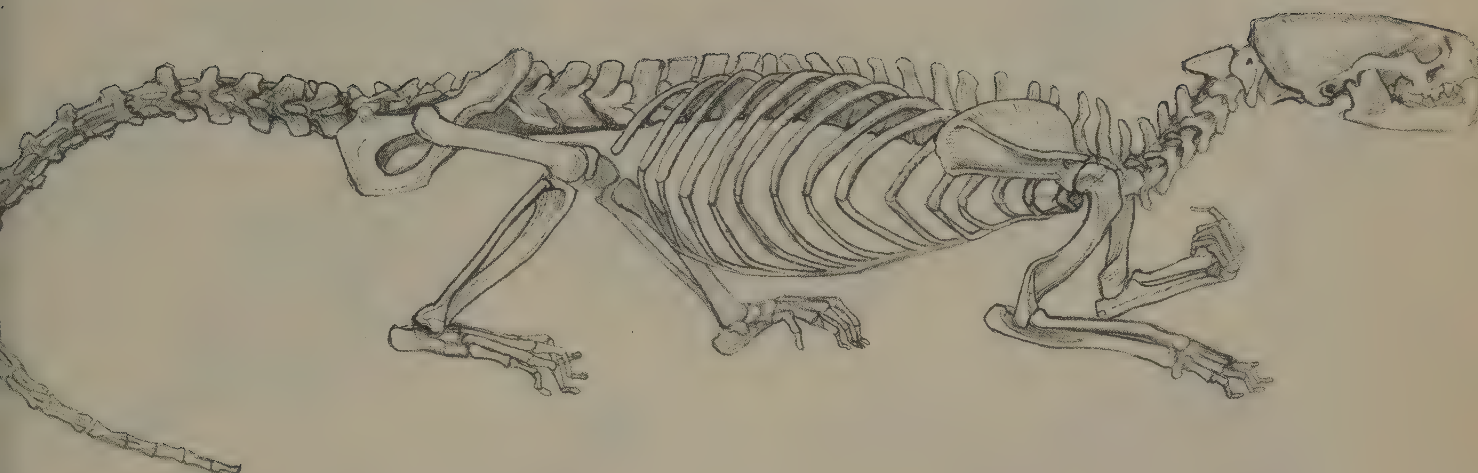
Less sociable than the spot-necked otter, this species is seldom seen in groups larger than four or five individuals and it seems likely that both sexes establish territories on which they remain for long periods. Three distinct groups of *Aonyx* were known to inhabit less than five kilometres of the wooded Ruanda Valley in south-western Tanzania for 25 years. An otter tends to walk over several kilometres of stream bed in the course of a single night but the two favourite areas of activity in the Ruanda River tended to be more restricted than this and these areas scarcely changed over the years until one of them became opened up to riverside cultivation. There were periods when more than one otter was present and one September there was a family of young and in another year a lactating female was killed with a club after a gang of large hounds had brought it to bay. The family, consisting of a mother and her young, had a holt within the tangled roots of some *Ficus* trees growing out of an eroded bend in the river. Down a nearby bank there was a well-worn slide into a pond. I do not remember noticing dung deposits that year but in subsequent years there were definite and limited stretches of bank less than a kilometre upstream that were littered with numerous droppings and one or two spots with accumulations next to well-trampled resting spots overlooking deeps in the stream. I did not learn the sex of the otter or otters making these deposits but the female chose to have her litter in the quietest, most secluded stretch of river for many kilometres. It is possible that the spatial distribution of these otters might resemble that described by Erlinge (1967a) for *Lutra lutra*, with single females well spaced out, while the more widely ranging males may associate with them until driven off shortly before parturition.

Shortridge (1934) describes them as being conservative. Prickett (1974) has described two of these otters visiting the pond in Yathabara glade every few months and staying for about a week before leaving again. This pond is a kilometre or so from the nearest stream but the regularity of their visits might imply some sort of home range circuit. Reports of attacks on chicken coops well away from water might concern similar circuits or else be made by subadults wandering after having been expelled by breeding females or territorial males.

Gestation lasts for about 63 days and there are two to possibly five young; it is uncertain whether these animals breed seasonally. Ansell (1960b) records births in July and August in Zambia; Mrs Nuti told me that she noticed young emerging in March and April in southern Uganda.

It has been reported that the left anterior teat does not develop in the female so that she has only five functional teats. Duplaix-Hall (in Ewer, 1973) reported that an otter carried any object against its chest and that it was predominantly the left hand that was used. Maxwell (1960) noticed, instead, that his pet usually used her right hand. The young are also carried in this way or in the mouth when very small, and the mother proceeds on three legs or occasionally may even waddle along on two, clutching her infant to her chest.

During the first months of life the young are hidden in a burrow, crevice, root or reed tangle and some sort of nest is made. Young open their eyes at



about four weeks and then begin to venture out with the mother. Their permanent dentition is acquired between the tenth and eighteenth weeks.

By the time the animal is one year old it has lost its pale undercolouring and woolly coat and it has acquired the crisp white bib and dark body of an adult. From observations on captives the pale baby belly appears to attract grooming by adults and it is possible that the white bib inhibits bites from being inflicted in a dangerous area, its signal function being a ritualized extension of the juvenile's appeasing posture lying on its back and presenting its pale vulnerable underside. It is interesting in this connexion that the bib becomes progressively darker with age until it no longer presents a strong contrast.

The young chirp incessantly and this might be an appeasing call; the adults, like all otters, make a loud contact whistle. Mild aggression is marked by a miaowing wail and at high intensity this breaks into a fierce bark which has been rendered as "kwa-a-a kwaaaa".

It is difficult to get a true idea of the status of this species. Its occasional

visits to the poultry yard give little indication of abundance, for most of the otter's foods are outside human interest and its nocturnal habits make it very inconspicuous. Although it may cause damage to some small fishponds or breeding tanks, this species is in no way a danger to the fishing industry nor to sport fishing and the nominal protection it is afforded at present is essential to discourage trade in the highly valued skins.

Stevenson Hamilton (1914) described seeing a wounded otter pounced upon by crocodiles; yet Shortridge (1934) saw otters splashing about close to crocodiles without coming to harm. Mrs Nuti found evidence of a monitor taking a young otter and it is conceivable that pythons, fish eagles or other birds of prey might occasionally take the young.

The nearest ecological competitor of the clawless otter is the marsh mongoose, *Atilax*, and it would be interesting to know what factors favour one or the other species in different habitats. The marsh mongoose is less aquatic and does not feed beyond the shallows, whereas the otter readily dives and investigates depths out of the mongoose's reach.

The spot-necked otter is known to suffer from leeches and it is possible that *Aonyx capensis* is also discouraged by these or other parasites which do not affect the mongooses. In recent years, Lake Naivasha acquired vast resources of crustacea, in the form of molluscs and introduced crayfish. In this and other localities *Aonyx* is inexplicably absent but *Atilax* is abundant. *Atilax* has a thin coat and is rare at higher altitudes and it may be that it excludes *Aonyx* from shallow waters at altitudes below 1,500 metres, leaving the otter to dominate the full span of aquatic habitats in the highlands, but restricting it to deeper waters at lower levels. An investigation of this problem might throw an interesting light on the nature of competition.

Viverrids

VIVERRIDAE

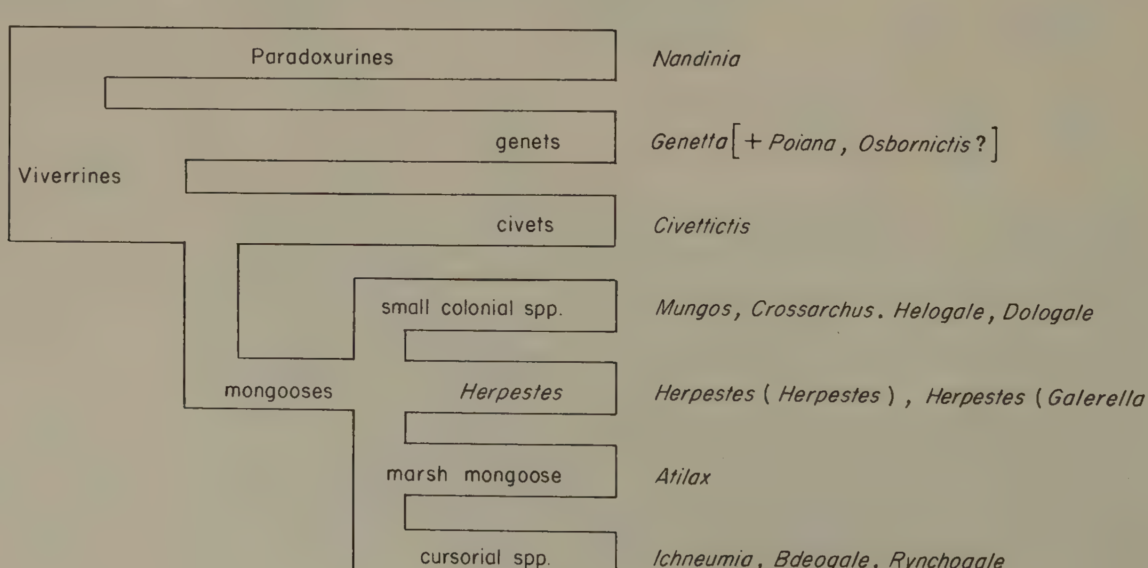
Viverrinae
Paradoxurinae
Herpestinae

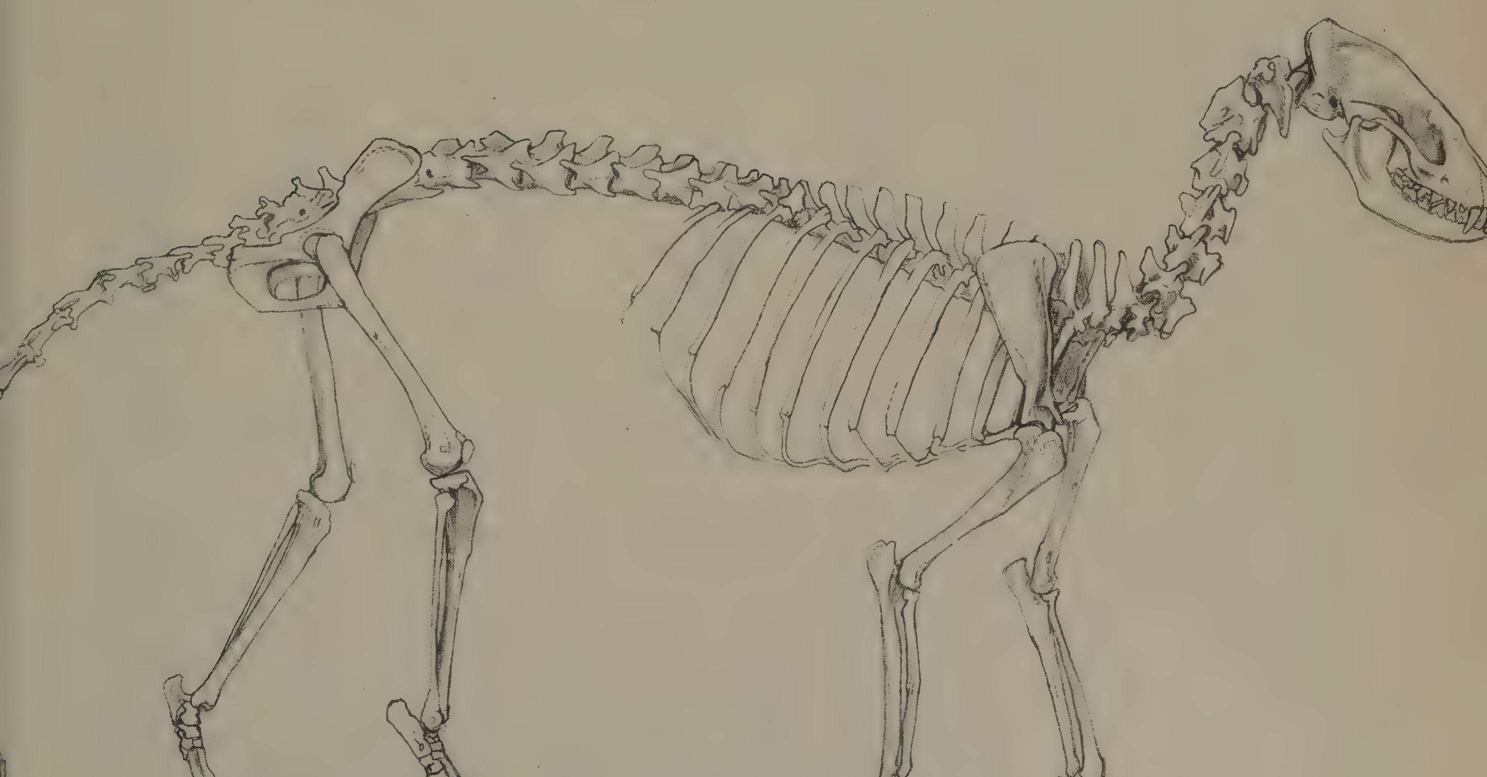
In the introduction to the carnivores I described the viverrids as offering us a glimpse of the earliest origins of the Carnivora. The viverrids are for the other living carnivores what the lemurs are for the higher primates. Because all the modern carnivores derived from a miacid stock, viverrids have special interest for the approximation they offer to the common ancestral stock of cats, dogs, bears, racoons and mustelids.

The viverrids are all of relatively small size and their teeth, although subject to highly significant adaptation in several genera, are conservative in structure. Of the thirty-seven genera eighteen are arboreal (the majority of these are oriental palm civets, a subfamily only represented in Africa by *Nandinia*). The terrestrial species are mostly herpestine mongooses which belong to a late and almost wholly African adaptive radiation.

The African viverrids are also interesting because they occupy the majority of small carnivore niches on this continent. Outside Africa many equivalent niches are filled by carnivores from different families so that some very striking convergences occur. Looked at in another way, the early radiation of carnivore families from the miacids has been partially recapitulated in a later radiation within the African viverrids. There are long lithe hunters with short legs (the weasel-like *Herpestes sanguineus*). There are soft-furred, hook-clawed arboreal stalkers (the cat-like *Genetta*). The so-called dog mongoose, *Bdeogale*, is ground-dwelling, omnivorous and cursorial. Like the procyonid racoon there is a semi-aquatic specialist in manual dexterity, *Atilax*.

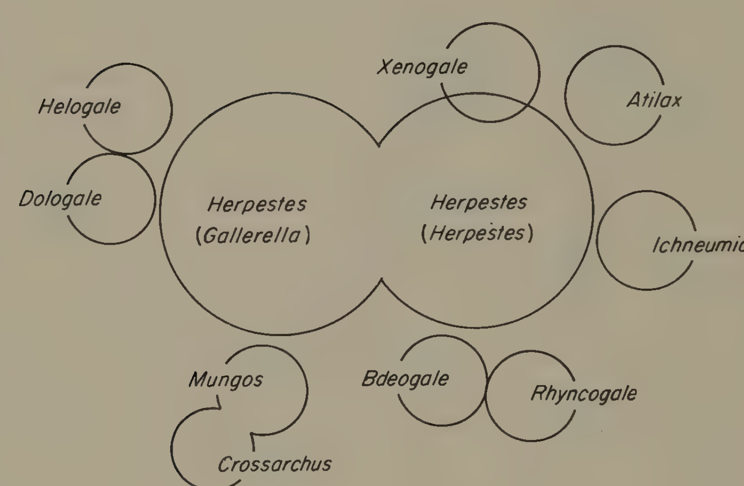
Hypothetical relationships of viverrid groups





Distinctly herpestine and viverrine fossils occur in the lower and mid-Miocene of Europe (Petter, 1969) so divergence at the subfamily level must have occurred very early.

The Miocene sees the first uncontested fossil viverrids in Africa (Savage, in press) and at least four lineages (paradoxurines, herpestines and arboreal and terrestrial viverrines) would seem to have entered the continent during the Oligocene or earliest Miocene. A single herpestine ancestor would seem to have given rise to all the genera of African mongooses, a radiation that has been discussed in some detail by Petter (1969).



Schema of hypothetical relationships amongst African mongoose genera (according to Petter, 1969)

Separation between the viverrines that are more arboreal (linsangs or genets) and those that are more terrestrial (civets) probably preceded their invasion of Africa. Both are represented in the Ethiopian and Oriental regions, however, here again some species of African genets might be recapitulating an earlier sequence by adopting more ground-dwelling habits.

Of the three subfamilies the palm civets, Paradoxurinae, might represent the most archaic. Surviving types are restricted to forest, are often highly specialized and there is even a semi-aquatic form among the nine genera in tropical Asia. Most of them are wholly or partially frugivorous and several are rare isolated forms on the brink of extinction. It seems likely that the oriental palm civets began their radiation and became established before the emergence of advanced modern carnivores, and their survival may have been assisted by fruit-eating, thus avoiding competition. It is therefore significant that this subfamily is only represented by a monospecific genus, *Nandinia* in Africa.

Adaptation to a variety of niches could have been inhibited by the presence of competitors and this would be consistent with the invasion of Africa by viverrids having taken place after the emergence of felids, mustelids and primitive canids.

Petter (1969) has used tooth structure to diagnose relationships within the Herpestinae. He has shown that *Herpestes* (in the large forms as well as the small-size *sanguineus* group) show the least modification of the tooth row from that of a primitive miacid-like carnivore. There is an interesting parallel here with the *Rattus*-like murids in that an ancient and conservative type appears to be the most widespread and successful (see Vol. II, p. 570) and the phenomenon may have a similar explanation.

Occlusion patterns in the cheek teeth of viverrids. Upper tooth row in black, lower row in white. Stipple: occlusal surfaces
Above: *Miacis, Miacis, Genetta, Civettictis, Nandinia.* Below: *Herpestes ichneumon, Helogale, Atilax, Crossarchus, Bdeogale, Rhynchogale.*

Most other lines have reduced the number of teeth or else their cheek teeth have been inflated and re-aligned to accommodate to different diets. The broad trend in African mongooses is away from cutting and shearing teeth, which represents retreat from a typical carnivore adaptation. Africa does not have as many species of canids, cats and mustelids as some other continents but those that are present are abundant and dominant in their own fields of specialization. Their presence may have placed limitations on the radiation of mongooses and the diversity of mongooses is probably best viewed in the context of the other small carnivores (see table, pp. 4 and 5).

Crossarchus

Mungos

The diversity of viverrid adaptations includes modification of proportions and limbs to totally different habitats and hunting methods. *Nandinia* is particularly muscular and is the most wholly arboreal of all the viverrids. Its limbs resemble those of cats. Only one mongoose, *Herpestes sanguineus*, makes a habit of climbing. *Bdeogale* has reduced its digits to four, the two central toes are larger and take most of the animal's weight. *Atilax* has very sensitive hands and has a highly developed sense of touch. The structure and breadth of muzzles are closely correlated with feeding habits and diet. For example, *Herpestes* and *Genetta* have pointed muzzles; they dart and snap with their teeth, but the latter also use their claws. *Mungos* manipulates most of its prey before eating as does *Atilax*. *Bdeogale* has a very broad muzzle and it feeds carefully and slowly. There are differences between genera in the degree to which the upper lip is cleft, which are presumably correlated with feeding.

Rhinaria and soles of feet
Left to right: *Atilax*, *Herpestes* (*Galerella*), *Bdeogale*, *Herpestes* (*Herpestes*)

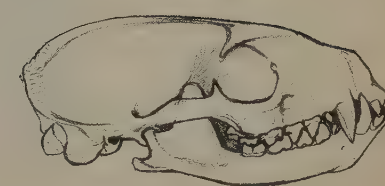
There are also considerable differences in facial expressions and in the intensity of their aggressive behaviour so that some appear fiery and others very lethargic in their responses to other animals and particularly to the stress of capture. Some of the mongooses are diurnal but the rest of the family is primarily nocturnal. Bernau (1969) found that the diurnal *Mungos* can discriminate colour, whereas *Genetta* cannot.

Sexual dimorphism is generally minimal and in several species the female tends to be dominant.

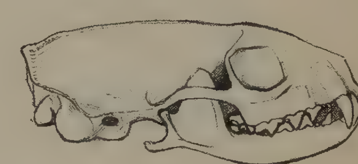
The majority of mongoose species are solitary foragers and are intolerant of company. Many form short-lived family associations but several genera have extended the family into a pack. Recent observations have shown that the socialization of these mainly solitary animals may involve difficulties that are only overcome by complex contrivances and that the demands of social life have led to some extraordinary details of behaviour (see p. 196).

Dologale

A fundamental mode of communication in viverrids is by means of scents. Many species have large perineal glands and these have been described in some detail by Pocock (1915a, b). In *Nandinia*, the perineal gland is a broad plate of naked skin underlain by dense glandular tissue. This plate can fold, so that a sachet is formed and the gland's muscular action presumably assists the marking of trees, branches (and possibly other palm civets). This primitive arrangement is greatly elaborated in the pocket-like glands of the genets. The secretions are so copious and durable in the civet that they once provided the perfume trade with a valuable fixative of flower scents. The mongooses, instead, have anal pouches which can generally be everted to expose the openings of anal sacs or cutaneous glands. There have been several reports suggesting that anal glands may be used as lures to prey. Their role in the development of luring behaviour is more fully substantiated and discussed in the profile of *Herpestes ichneumon*.



Bdeogale crassicauda



Herpestes (*Galerella*)

Mongooses are a minor nuisance to poultry keepers but their main significance for human affairs is as hosts or reservoirs for diseases that can affect man or his pets, the main danger being rabies. They themselves are increasingly popular as pets.

Civets and Genets

Viverrinae

The peculiarities of this division of the viverrids have been outlined in the viverrid profile and a recent diagnosis is available in Rosevear (1974). The most obvious characteristics of the group are their spotted coats and, in the genets, soft fur and retractile claws.

Genets (Genetta)

Local names

Kanu (Kiswahili and many other languages), Nghanu (Kigogo), Nyamanu (Kichagga), Akasimba (Luganda), Nsimba (Lubwizi), Eisembe (Lukonjo), Anyara, Cwiny (Lwo), O lo (Lugbara), More (Kiliangulu), Mwowu (Sebei), Lunziri (Lugisu), Kumondo (Lubukusu), Kiradongo (Luragoli), Bhitarongo (Tiriki), Emeris (Karamojong), Alisabat (Ateso), Tondolega (Kihehe), Kandidi (Kinyamwezi), Ludindi (Kitaita), Ndele (Kinyaturu), Nilele (Kiramba), Magarok (Masai)

Species

Genetta genetta
Genetta tigrina
Genetta servalina
Genetta victoriae

The genets probably represent one branch of a primary radiation of the Viverridae. The principal specialization has been towards an arboreal habit, with climbing limbs, bifocal vision and the improved co-ordination that go with it. While birds and rodents are common foods, they are equally ready to eat insects and fruits, so colonization of the arboreal niche was not linked with a specialized diet. The recipe for success in this niche would seem to be relatively exacting; for small arboreal omnivores occur in tropical areas of all continents and in every case resemble the genets remarkably closely in spite of belonging to totally unrelated groups. Thus there is the spotted marsupial *Dasyurus* in Australia, the Procyonid cacomistle, *Bassariscus*, in Central America, the linsang, *Prionodon*, in South-east Asia and the *Fossa* of Madagascar. Although the last two genera are also viverrids, they represent distant branches that have been separated for at least twenty million years; yet their resemblance with the genets is astonishingly close.

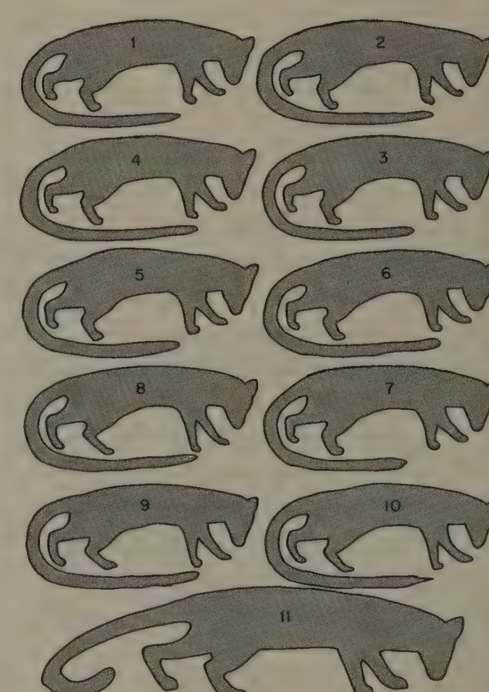
The study of genets has implications for the evolution of the felids and this is discussed elsewhere (p. 303). The lack of dietary specialization in the genets is linked with a rather mild disposition and relatively clumsy killing techniques in spite of the rapidity of their movements. They turn readily to fruit or insects, both of which are plentiful for much of the year in tropical Africa, and the restricted range of *G. genetta* in Eurasia may be due to a lack of "buffering" by fruit and insects during the winter which brings them into direct competition with specialized killers belonging to the felid and mustelid families. It is quite common for domestic cats to kill and even eat genets and there is at least the possibility that the wild *F. sylvestris* would be equally ready to do so. The killing bite of a cat is a particularly accurate and deadly specialization. The genet, however, relies on speed, agility and its cryptic colouring to catch its food and also for defence—the effectiveness of all are likely to be reduced in a northern hemisphere winter—and, despite its rapidity, the genet's performance as a killer is decidedly inferior to a cat's.

In Africa a broad range of potential foods is available in all types of wooded country and the genets are amongst the commonest of all carnivores. To

Genetta servalina

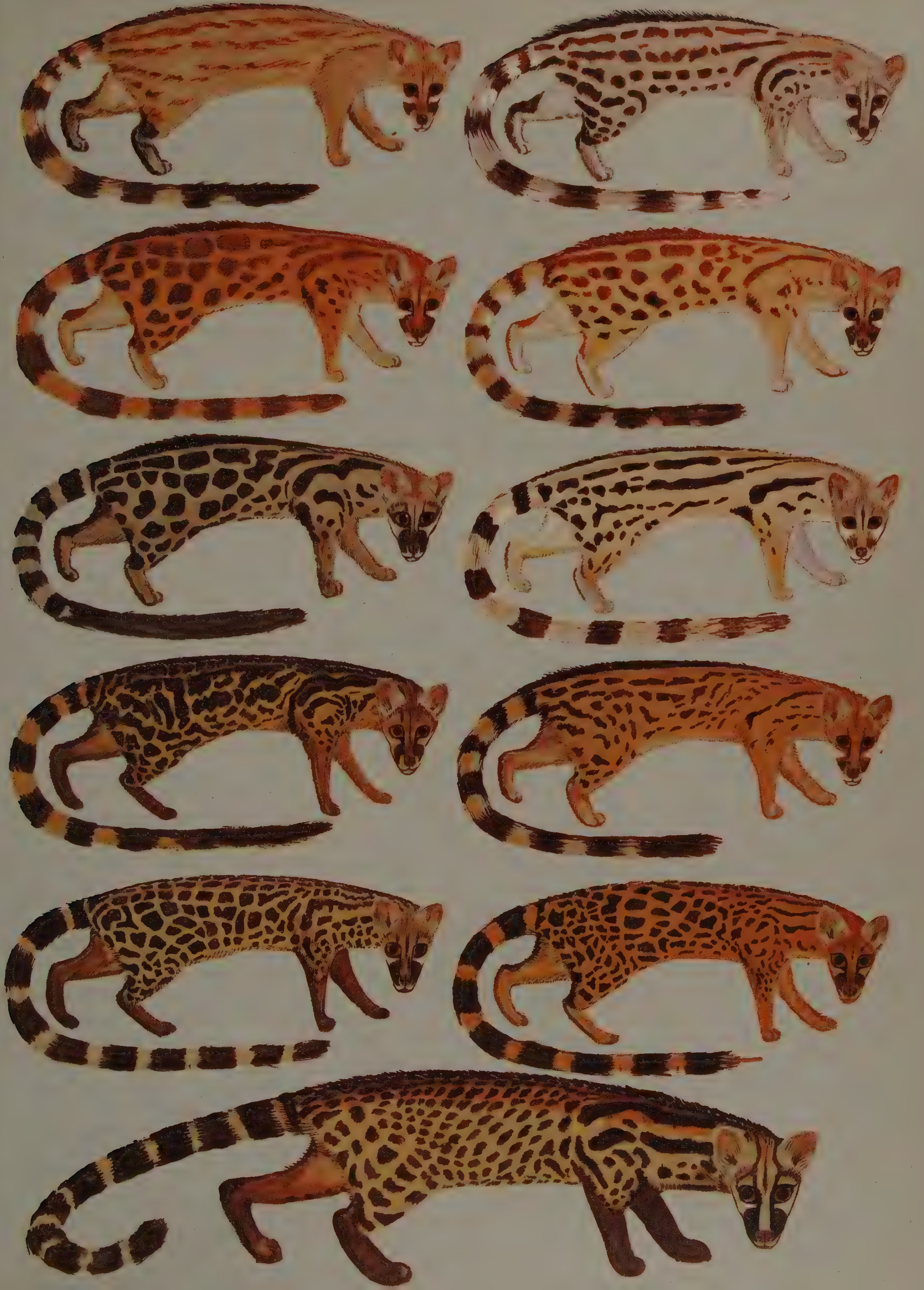
exploit the whole spectrum of wooded habitats the genets have radiated into a number of ecological species. Although there are localities in which at least three species can be found together, their niches are fairly distinct.

Genetta servalina is a true forest species with a discontinuous distribution. *Genetta genetta* is a form adapted to arid areas which is dominant in all the drier habitats and well able to live amongst boulders in areas without water. *Genetta tigrina* is by far the most widely distributed form; it occupies a variety of habitats and overlaps both the former species extensively. Less able to do without water than *G. genetta* and possibly rarer in high canopy closed forest if *G. servalina* is present, it dominates all habitats in between these extremes and has adapted particularly well to cultivation and human settlement.



Genetta

(1) *Genetta genetta pulchra*
(4) *Genetta tigrina stuhlmanni* (colour variety)
(5) *Genetta tigrina stuhlmanni* (colour variety)
(8) *Genetta servalina bettoni* (aberrant pattern)
(9) *Genetta servalina intensa*
(11) *Genetta victoriae*
(2) *Genetta genetta senegalensis*
(3) *Genetta tigrina rubiginosa* (or *suahelica*)
(6) *Genetta tigrina deorum*
(7) *Genetta tigrina aequatorialis*
(10) *Genetta servalina lowei*



Genetta victoriae is a larger animal restricted to the Rain forests of the Central Refuge and it probably represents something of a relic species, occupying a niche in the forest that may be intermediate between the smaller genets and the civet.

In zoos *G. genetta* and *G. tigrina* have been hybridized (Gray, 1971) although this is so far unrecorded in the wild.

Although patterns and details of proportion differ, all the genets have a strong superficial resemblance and the Karamojong aptly describe them as "rat-like leopards". They all share a black and white ringed tail and a boldly patterned face. Animals from totally different families and orders have evolved similar signalling devices on their faces and tails, notably the primate, *Lemur variegatus*, various cats, *Felis*, and the procyonid cacomistle, *Bassaricus*. All these species live in well-wooded habitats and their social or sexual life is well served by these spectacular devices. Curiously enough, melanistic individuals are not uncommon, particularly among *G. tigrina* in some montane localities (Webb, 1947), so it seems that tail and other visual signals are dispensable in some circumstances.

Like the civet, genets have small perineal musk glands in addition to the powerful and foul smelling secretion of the anal glands.

The catholic diet of all genets has already been mentioned. They eat small mammals, especially rodents, but also shrews, bats, galagos, birds and their eggs, frogs, millipedes, centipedes, scorpions and various fruit and, while they may feed predominantly on one or two types of food at certain times of the year, it is not uncommon to find stomachs containing a variety of food eaten in a single night. The genet eats whatever is most available, although I have found all three species particularly susceptible to freshly killed birds as bait. Carpenter (1970) and Webb (1947) found no difficulty in catching females on their latrine sites. Once caught, they are silent and during daylight at any rate, may even tolerate cautious stroking within a day or two, although wild-caught adults do not in my experience become really tame.

Their scent glands are clearly capable of conveying various types of information relating to their sexual, social or territorial behaviour as well as being used as a deterrent to enemies. When angry, frightened or damaged, a genet exudes a foul-smelling yellow secretion from the anal gland and, if unable to escape, it lies on its back trying to defend itself with all its claws and teeth. The defensive position is interesting as birds and mammals are often killed by the genet using all its limbs and teeth at once, falling over on its side and chewing away at the head, neck and throat of its prey, while clawing and kicking. Their grooming behaviour has many resemblances with that of the Felidae and they also scratch-mark with their claws, miaow when courting and purr like cats. However, they also have a very viverrid manner of glandular marking while adopting a handstand.

Although mainly nocturnal, genets are often active during the day in the rainy season. During the day they may seek security in hollow trees, termitaries, rocks or eagles' and hammerkops' nests, roofs, empty beehives or even in quite exposed vegetation and I have seen one sun-bathing in the upper layers of a dense thicket tangle. There are sexual as well as specific differences in the choice of resting sites, with females showing greater attachment to specific refuges.

Genets are primarily solitary animals. Carpenter (1970) studying a *G. tigrina* population in South Africa found that the females are territorial but males are not. Four out of six trapped females homed to their territories after being transferred 10 and 32 km while males tended to remain where they were released and they are probably not attached to specific areas. Judging from the behaviour of captives, it would seem that females probably defend their territories, for adult captives will fight fiercely if put together.

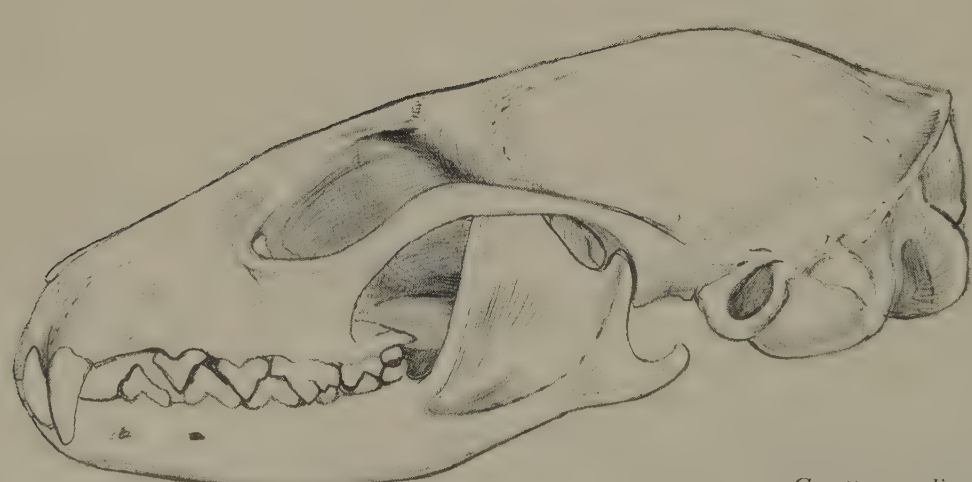
Volf (1965) bred eight generations of *G. genetta* in Prague Zoo and remarked that the male must be separated before parturition if the young are not to be eaten. That the young or even the female may be treated as prey by the male was shown by a male's killing a female, with which he had lived for two years, immediately after killing some rats.

A wild female *G. tigrina* lived in the roof of our house in Tukuyu for many months and was only briefly seen with another adult, and when her three young were agile enough they followed her out in close single file along an identical route every evening at dusk.

A single dung site is visited regularly, but Rowe-Rowe (1971) found urine was deposited in several places and a captive *G. tigrina* presented with a stuffed genet sniffed it and urinated on it, while swaying from side to side.

Fiedler (1957) studying captive *G. tigrina* noted a spontaneous increase in glandular activity in two male genets which coincided with two supposed mating peaks or seasons. They made handstands and he mentioned them staining two places of their cage only, renewing deposits immediately after the keepers cleaned the cage.

The genet becomes vociferous when mating. What controls the timing of reproduction is not known and no detailed study of the natural history of a wild population has been attempted to date.



Genetta servalina

Genetta tigrina

A male initiates courtship with grumbling calls as he follows along behind a female. Eventually the female answers his call and allows him to come into closer contact. Up to this time the female's tail and hindquarters are kept low and she constantly turns away from him or even flees but his persistence is rewarded and they start to rub cheeks, interspersed with much sniffing and examining of faces and genitalia. The female now raises her tail vertically and eventually invites copulation by raising her hindquarters while crouching on her forelegs with her tail to one side. Dücker (1962) has described copulation in detail and points out the cat-like posture of the male, which stands on stretched legs over the female, only biting the nape, mongoose-style, at the end of the copulation, which generally lasts about five minutes and is accompanied by much miaowing. Mating is followed by some excitement on the part of the female who drags her anal glands and rolls on her back; both sexes lick their genitals for a while.

Gestation lasts 70–77 days (*G. genetta*, Volf, 1965) and there can be two litters a year; up to four young are born—usually two or three. Some breeding is going on all year but there seem to be birth peaks in some populations.

The kittens are born with sealed eyes and ears and covered in grey fur in which the pattern, although present, is blurred and indistinct because the light and dark tones of the relatively long fur are rather close. The tail is rather short and only partially ringed. Both the rings and the length of the tail develop rapidly. Eyes and ears open at about the tenth day (5—18). The mother stays with her kittens for long periods and she licks away all the excreta like a cat. When carrying the young, the mother usually grips their

curled form across the small of the back. The kittens have a piping mew and will hiss or spit when alarmed. The canines erupt when the kitten is about a month old and it starts to take solid food about two weeks later. Dücker (1957) noted the young sucking saliva from the corner of the mother's mouth at this time and the young take progressively more food from the adult but continue sucking for many months; some females stop lactating as late as six months after giving birth. They are mature at two years and have been known to live 34 years in captivity (Michaelis, 1972).

When they are threatened, the fur stands on end and, like a cat, they arch their backs but the range of facial expression is very much more limited.

From the Greek empire up to the Middle Ages, when the domestic cat, *Felis catus*, became established in Europe, *G. genetta* is thought to have been the main domestic rat-catcher and it features in the tapestries of the period (Bouillant and Filloux, 1955). In North Africa genets were kept by the Ancient Egyptians and they are still kept by the Berbers. It has been suggested that they were relinquished in favour of the cat because of their smell (Michaelis, 1972) but it seems more likely that the common cat was not only better at killing rats but was also able to kill genets.

Opposite: *Genetta tigrina*

Common Genet (Genetta genetta)

Races

Genetta genetta senegalensis	East Africa, north of Rufigi
Genetta genetta pulchra	South of Rufigi

This species is recognizable by its very prominent dorsal crest, which runs from the shoulder to the base of the tail, and by its coarse long hair. The spots have a more emphatically linear arrangement, running in three or four lines from the shoulder. The tail tip is usually white but not invariably so. The skull tends to lack a sagittal crest and the post-orbital process is poorly developed.

The colouring within races of *G. genetta* seems to be less subject to variation than in *G. tigrina* and the two patterns figured at the top of the colour plate (facing p. 138) are typical of their respective races.

The common genet ranges very widely through the savannas of Africa right up to the edges of the Sahara and along the north-African littoral. It is found in Spain, up to Belgium and southern Germany, in the eastern Mediterranean Israel and Arabia. Below the Sahara there are two major populations, the northern one ranging from Senegal to Somalia and Kenya, the southern one from the Orange River in the Cape to southern Tanzania. The boundary between these extensive ranges is the Rufigi River and this distribution is another example of the importance of this river in the zoogeography of Africa (see Vol. II, p. 3).

World distribution of *Genetta genetta*

This species is an inhabitant of the drier bush and woodlands, particularly areas where there is a severe dry season. In many areas it co-exists with *G. tigrina* but it will generally be found on the higher, often rocky ground where water drains off quickly, leaving the place waterless for a large part of the year. Thus a typical distribution of this species is on escarpments, rocky outcrops and other hills, while *G. tigrina* is found in the moister valleys.

It is the security and shelter provided by rocks, as well as the food resources that cluster in the associated thickets, that encourage this species. Almost any site of this nature is likely to be inhabited by *G. genetta*.

A great proportion of this animal's time is spent on the ground and it is likely that seasonal changes in diet are more marked in this species.

In Europe, *G. genetta* has a birth peak during the spring (De la Fuente, 1972) but breeding is known to occur throughout the year and in Prague Zoo they bear two litters a year, mostly in spring and autumn.

In central Tanzania a litter has been found in mid-November.

Genetta genetta

G.g senegalensis (includes *neumanni*)

G.g pulchra

NOTE *Genetta genetta* is very rare towards the western margins of its range

Genetta genetta senegalensis

Common Genet (Genetta genetta)

Family Viverridae
Order Carnivora

Measurements
head and body
50 (42—63) cm
hindfoot
8·8 (7—9·7) cm
tail
46 (39—53) cm
weight
2 (1—2·3) kg

Blotched Genet (Genetta tigrina)

Family Viverridae
Order Carnivora

Measurements
head and body
53 (49—60) cm
tail
42—54 cm
hindfoot
9 (8·5—9·8) cm
weight
1·8—3·2 kg males
1·3—2·6 kg females

Blotched Genet (Genetta tigrina)

Races

Genetta tigrina rubiginosa	Tanzania
Genetta tigrina stuhlmanni	Southern Uganda and southern Kenya
Genetta tigrina aequatorialis	West Nile
Genetta tigrina somalica	North-east Africa
Genetta tigrina mossambica	Southern Tanzania

G. tigrina has a shorter dorsal crest and fur than *G. genetta* and its skull is more robust. The tail is always dark-tipped and the legs are short. There are a number of regional populations in this very widely distributed species which inhabits a greater variety of habitats within tropical Africa than the other genets. Ecological differences are reflected in lighter tones and more open patterns in populations from dry areas and in darker, more boldly patterned animals from areas of high humidity (see plate). However, nomenclature is complicated by the existence of polymorphism, differently coloured morphs occurring in the same area. Predominantly red or grey animals have been seen as pairs and are likely to be present within a single litter. These extremes are illustrated in figs (c) and (e). Intermediate forms show variable amounts of orange blotching on a grey background.

Colour variation is particularly conspicuous in the very large-blotched type which ranges across southern Uganda and Kenya to the moister areas of northern Tanzania, *G. t. stuhlmanni*. This distribution pattern approximately coincides with the last major forest expansion (see pp. 30, 70, Vol. I). The Albert Nile appears to mark the eastern boundary of a weakly-marked northern savanna type, *G. t. aequatorialis* (h).

From coastal Kenya southwards to the Cape there is the *rubiginosa* type.

In southern Kenya and northern Tanzania, where the distributions of these two forms overlap, somewhat intermediate forms have been recorded, suggesting that some mixing takes place between *stuhlmanni*, dominant in the more montane and forested areas, and *rubiginosa* in savannas, woodland and gallery forest. The so-called subspecies, *suahelica* and *erlangeri* come from this overlap zone. The light-coloured Somali genet (f) has adapted to very arid conditions and a comparative study of the ecological separation between this form and *G. genetta* in the same habitat would be most interesting. It has been suggested that *G. genetta* and *G. tigrina* separate along a 63·5 mm rainfall isohyet (Taylor, 1970), but this is by no means consistent and there are very extensive areas of overlap. This species is more arboreal than *G. genetta*; I have frequently picked up their eye-shine in the trees with a torch and they often rest up in trees during the day. They are also most adept climbers, racing along trunks and over thin branches with equal assurance.

They are found in all East African forests but in several restricted localities, i.e. Budongo, Kalinzu, Bwindi forests and the montane forests of the Ruwenzoris and Mt Elgon sight and trapping records suggest that they are less common within the forest proper than *G. servalina*.

Cultivation and gardens provide ideally mixed conditions for *G. tigrina* so that this species is quite the most familiar of the East African genets. The range of foods taken by this species and *G. genetta* scarcely differ at all but the most easily available foods in their respective habitats are not the same and the species could be predicted to have evolved different preferences.

Smithers (1971) collecting large numbers of both species in an area of overlap in Botswana has confirmed this by documenting the occurrence of food items in 78 *G. genetta* and 30 *G. tigrina* stomachs. Over half the items were made up of a very wide variety of invertebrates but the most bulky foods in about half the sample were small rodents and the occasional bird; this applied to both species. The ecology of *G. genetta* was reflected in the rarity with which fruit was found, a relatively large proportion of reptiles and amphibians and a predominance of scorpions and Orthoptera in the diet. *G. tigrina*, instead, ate more fruit and fewer reptiles, while Coleoptera and Orthoptera were preferred insects.

PERCENTAGE OF MAJOR FOOD ITEMS

Species	Invertebrates	Small rodents and birds	Reptiles and amphibians	Fruit
Genetta tigrina	62	25	3	8
Genetta genetta	56	28	10	0·6

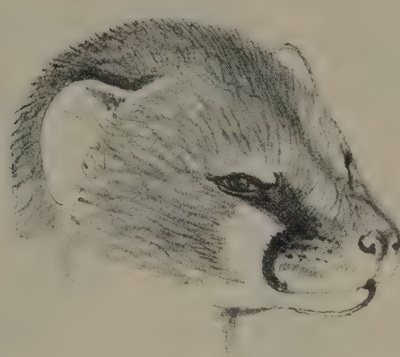
Where Smithers collected a small series in the same locality within a few nights of one another, *G. tigrina* was feeding almost exclusively on small rodents, while *G. genetta* was also taking a variety of invertebrates and reptiles. *G. tigrina* is often attracted to the moths, beetles and grasshoppers that assemble around street lights and other lamps. Prickett (1974) has seen them chasing hares but without success. Almost wholly nocturnal, temperature and cover might influence the activity of this species. Smithers (1971) has remarked that *G. tigrina* was not found abroad before 8.30 p.m. in Botswana, yet animals from the East African highlands often emerge at dusk and occasionally, on cool evenings, a little earlier.

Adults are solitary except when the young accompany their mother and over the period of courtship.

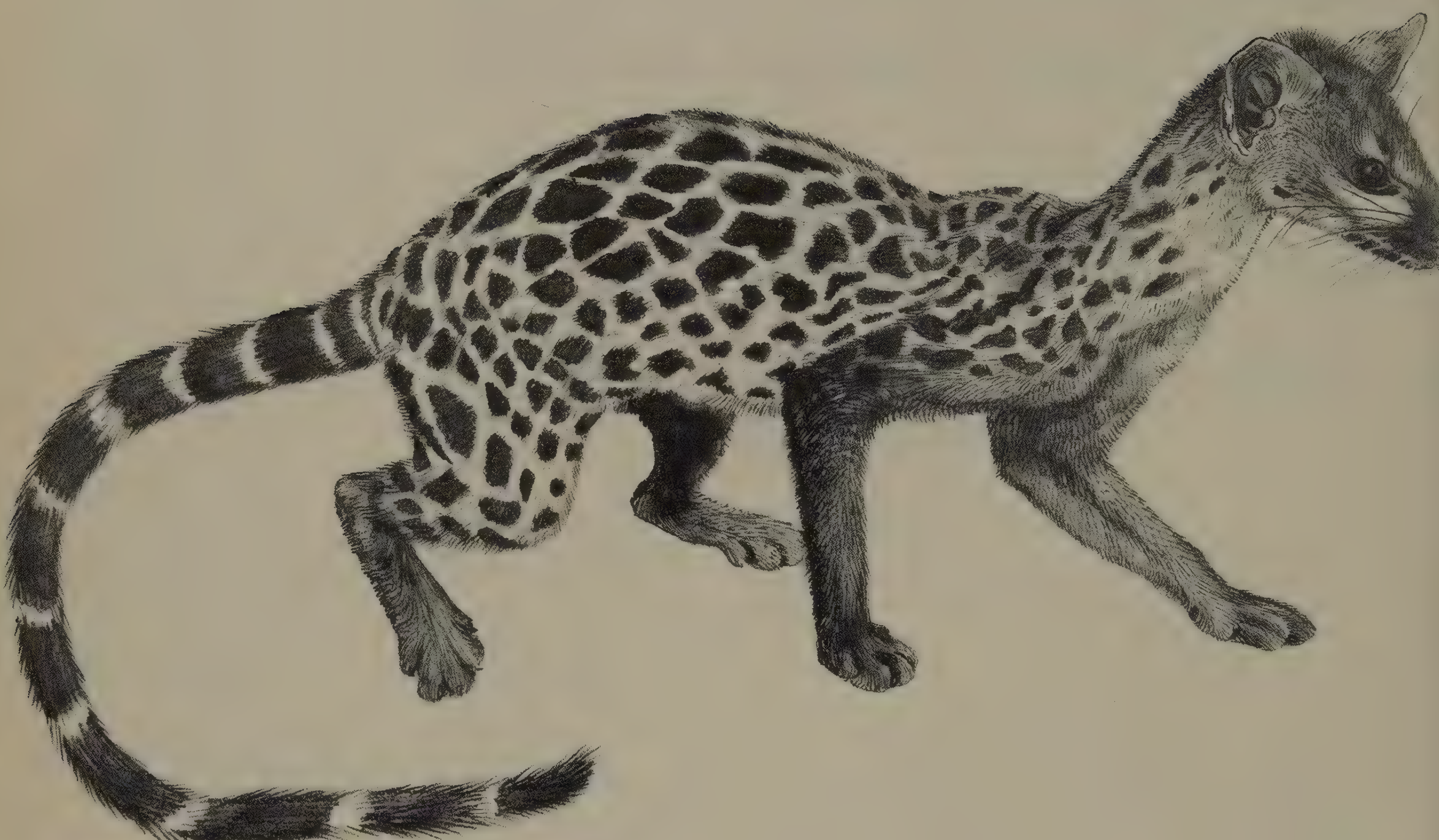
Carpenter (1970) found that individual females could be caught repeatedly within a limited area and he trapped five females at their dung deposits, whereas only one male was caught at such a site. When Carpenter released animals well away from their original trap sites, several of the females returned to their distant territories whereas males did not home and some were subsequently trapped again in the area of their release. When genets were caught in poultry yards the majority were males. A female might be retrapped after developing a taste for hens but Carpenter noted that a female only raids within her own home area.

The vocabulary of genets has many resemblances to that of cats; they purr, mew and miaow under similar circumstances and they also hiss and "spit" but they make a distinctive churring noise in distress and Rowe-Rowe (1971) has described a captive yapping at strangers.

Scattered breeding records imply that some breeding continues throughout the year in East Africa but Smithers (1971) found no evidence for *G. tigrina* breeding during the colder months of the year in Rhodesia and records indicated a prolonged breeding season from August to February.



Kitten



Servaline Genet (Genetta servalina)

Family Viverridae
Order Carnivora

Measurements
head and body
41—50 cm
hindfoot
7—8 cm
tail
35—44 cm
weight
1—1·12 kg

Servaline Genet (Genetta servalina)

Races

Genetta servalina intensa	West Uganda
Genetta servalina bettoni	Mt Elgon to Mt Kenya
Genetta servalina lowei (provisional name)	Southern Highlands

Genetta servalina

Genetta servalina

The servaline genet is very readily recognized by a narrow face, the absence of dorsal crest and relatively long legs. The fur is short and very soft with numerous spots so that the light background colour assumes more the character of a linear network over a dark ground, this is particularly true of *G. s. intensa*. *G. s. bettoni* and *G. s. lowei* have a yellower base colour. The latter form is only known from Dabaga where it was collected by G. Willoughby Lowe in 1932 (B.M. No. 33.8.1.20) and it is provisionally treated here as a distinct race, because neither its pattern nor its provenance allow it to be included with any other known form. As can be seen from the colour plate (10) facing p. 138 the pattern is very open and the ground colour peculiarly orange and even the white facial spots are suffused with this orange tint. The legs are unlike those of all other races in lacking any trace of dark colour. An interesting aberrant pattern is shown (8) same colour plate, from an animal collected on Mt Kenya, where melanistic examples are also known. This joining up of spots to give a marbling effect makes an interesting comparison with leopards and cheetahs (see pp. 350, 398).

This genet occurs throughout the Congo basin forests to Nigeria but its East African range is discontinuous.

Known from various West-Uganda forests, there seems to be a gap in central Uganda before it turns up again on Elgon, at Kaimosi, the Mau and Mt Kenya. The southern Highlands record is very isolated but further collecting would probably extend the range of this species somewhat. On Mt Elgon this animal has been recorded from 1,950 to 3,500 m and appears to be particularly numerous at an altitude between 2,100 and 3,000 m. It is also dominant at similar altitudes in Kigezi and Ruwenzori.

Rahm (1966) noted this species as very common in the Irangi region and he stated that it is more tree-living than *G. tigrina*. Judging only on the basis of where I have seen and trapped them I would think that the opposite might be the case but it is certainly true that *G. servalina* is more of a true forest form.

I have frequently seen this genet, like *G. tigrina*, foraging on the ground and it is often trapped there. A tree hyrax, various ground-dwelling rodents, some insects, birds and fruit are recorded foods.

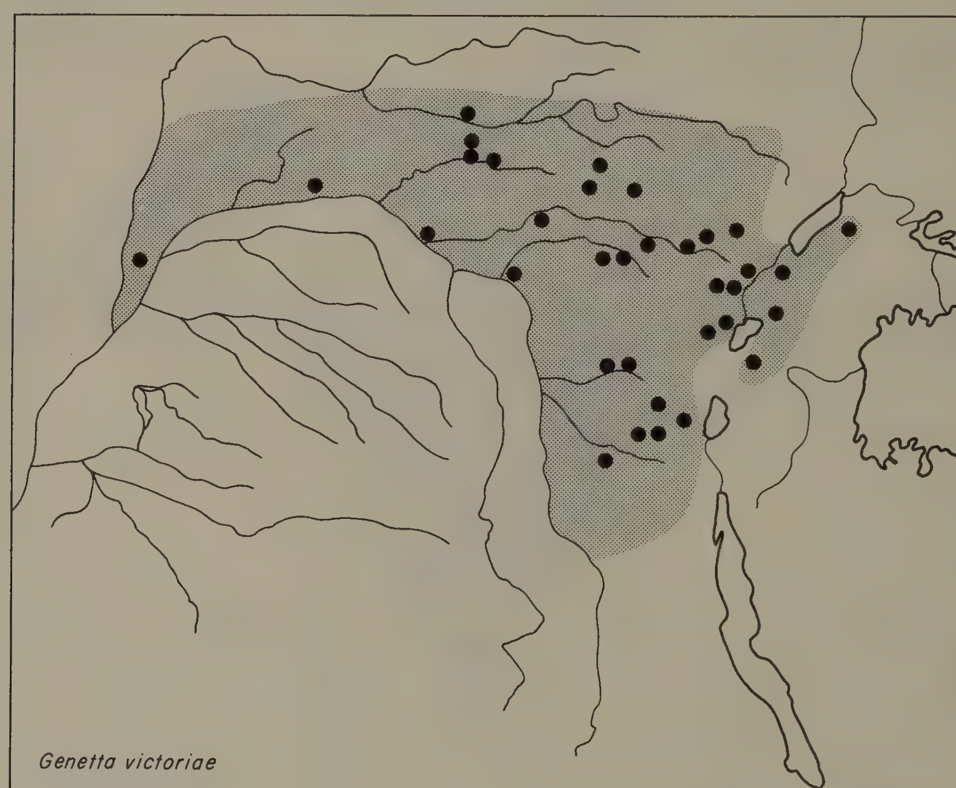
Breeding records from Uganda are: February 16th—two kittens—March 6th—seven small foetuses—June 5th—one full-term foetus and August 5th—date of a birth.

Giant Forest Genet (Genetta victoriae)

This large genet is marked with numerous small spots and has a soft even fur like that of *G. servalina* (colour plate (11) facing p. 138).

This species was named in London on the mistaken assumption that the specimen came from Entebbe on the shores of Lake Victoria, where the collector Sir Harry Johnson had his headquarters. In fact, like the okapi, this animal originated from the Semliki-Ituri region, which was within Uganda at that time and a centre of Johnson's interest in natural history. It is a true high forest species and occurs in several lowland forests in west Uganda.

According to Rahm (1966) it is very rare in montane areas. He kept one in a cage with *Atilax* and two *G. tigrina* without the animals fighting. It



Giant Forest Genet (Genetta victoriae)

Family Viverridae
Order Carnivora

Measurements
head and body
57—57·5 cm
hindfoot
9·8—10·2 cm
tail
44—44·8 cm
weight
2·5—3·5 kg (approx.)

was strictly nocturnal and slept in a box one metre off the ground. It fed on a mixture of rodents, bananas and rice.

I once saw this species trotting along a forest road at about 10.30 p.m. and thought momentarily that it was a civet. It is much more delicately built, however, and its short fur gives it a sleek appearance.

Nothing is known of the biology of this species.

Poiana

African Linsang (Poiana richardsoni)

This rare genus may occur in some West Uganda forests but there have been no confirmed sightings.

Osbornictis piscivora

Aquatic Civet (Osbornictis piscivora)

This rare piscivorous viverrine occurs in the Semliki Valley but has not yet been recorded from the Uganda bank. It might occur in Bwamba and also in North Kigezi.

African Civet (Civettictis civetta)

Family Viverridae
Order Carnivora
Local names

Ffungo (Kiswahili and many other languages), Lifungufungu (Kibena, Kipangwa), Ifungo (Kipare), Livungo (Kingoni), Lihungo (Kingido, Kimatengo), Ligunyuli (Luhya), Ntungo (Kinyamwezi, Kisumbwa), Nchungo (Kirangi), Nhungo (Kisukuma), Hungo (Kimatumbi), Enfumbe (Lusoga), Ffumbe (Luganda), Odumbere (Lugbara), Laboroto (Madi), Rujuguta (Runyambo), Ekiruzuguta (Runyankole), Ekitamujuguta, Tabunzuguta (Lunyoro, Lutoro), Woranget (Elkoni), Kitende (Lukonjo), Azamo (Kuamba), Kijamo (Lubwizi), Mpakone (Kimeru), Kitondalinga (Kihehe), Kisege (Kitaita), Nthee (Kikamba), Ndesi (Lugisu), Mugis (Sebei), Ol pilis (Masai), Chepkilis (Kalenjin), Giliri (Lwo, Karamojong), Ekwaru (Ateso), Shawaad (Kiliangulu)

Measurements
head and body
68—89 cm
tail
44·5—46·3 cm
weight
12 (7—20) kg

African Civet (Civettictis civetta)

Civettictis civetta

In terms of its diet and the build of its body the civet is a remarkably unspecialized mammal. It will live wherever there is cover, will eat almost anything and will take advantage of any kind of shelter. It is not a fast runner nor is it adept at climbing, but it is agile and elusive enough in thick vegetation.

Dense habitats reduce the importance of long-range vision and the civet does appear to be relatively short-sighted, but its hearing is acute while scent is undoubtedly the key sense, informing it of its surroundings and conditioning all social contacts with other members of its own species.

For several millennia the most important characteristic of the civet so far as mankind is concerned has been the possession of remarkably large scent glands under the tail, the secretion of which supplies a fixative for flower perfumes. So copious is the flow from these glands that it can be spooned out of the large orifice several times a week. Captive African civets have supplied the perfume industry of the Middle East with musk since Biblical times. Civets were exported together with ivory, wood and slaves and large numbers were kept in Ethiopia and Zanzibar until the relatively recent displacement of natural musk with chemical substitutes. All musk substances are capable of being impregnated with essence of flowers or other aroma but the remarkable property of civet musk is its persistence, for natural civet will give out an odour for several years. The value of this to the perfume trade has been obvious since the days of Solomon; its significance in the life of the civet remains to be investigated.

Even a casual acquaintance with the living animal in its natural surroundings betrays the dominant role of the glands and their secretion in its life. Following established paths, the civet walks with nose trailing close to the ground. The rump is usually carried higher than the head and at suitable trunks, stumps, stones or thickets, particularly at the junction of pathways, the animal stops, sniffs, slowly raises its head, turns round and, deflecting its tail, places a scent smear that is about 30—40 cm off the ground. An examination of the site shows that the smear is one of a series all at about the same height. When more than one civet is kept in a pen, the placing of a deposit by one animal is very soon discovered and overlaid by the other and there can be little doubt that civets can recognize individuals by their scent and that deposits convey olfactory information about the sexual and hormonal condition of other civets using a marking site.

The typical high-rumped, low-headed stance of the civet is probably influenced by the species' adoption of scent as the means of orienting its social and sexual life. The low carriage of the head also allows the civet to be extremely inconspicuous as it glides or trots silently along its path, for the black spotting, striping and mottling of the tawny-grey body and tail are excellent camouflage. From time to time or at any alarm the civet stops quite still and then cautiously raises its head. This brings into sight the black and white markings of the face which, from a frontal view, have the configuration of a target roundel. This pattern has an extraordinary resemblance with the

facial mask of the canid tanuki, *Nyctereutes*, in Asia and the Procyonid racoon, *Procyon*, in the Americas. What are the common features of their biology that could lead to such a remarkable convergence of pattern in three totally unrelated animals on four continents?

Although *Nyctereutes* is frequently solitary, it does form pairs and small family groups. Kleiman (1967) believes that its facial markings serve to attract attention to the face for social grooming. *Civettictis* is more frequently solitary and there is no evidence of intense facial grooming, so this would not provide an explanation common to the three species. All three are nocturnal inhabitants of thick cover, silently foraging, for the most part on their own, for whatever animal and vegetable foods are easily available. All are relatively abundant in appropriate habitats. Because they forage silently at night and in thick cover, there is also an increased likelihood of surprise encounters with other animals, including prey, predators and conspecifics. The first is an advantageous situation for any carnivore; the consequences of the last will depend on the circumstances and on the social pattern of each species but, irrespective of whether conspecifics are to be sought out as potential mates or avoided as competitors or rivals, there are obvious advantages for an accurate discrimination between conspecifics and other species before the animals come into physical contact. Considering the evolution of this pattern it should be remarked that all three carnivores have simple conical faces and their dark, pointed noses are a natural centre-focus while the dark eyes provide another natural starting point for the elaboration of a dark band.

A series of alternating black and white markings has the virtue of geometric simplicity, lack of ambiguity and high visibility in poor light conditions. In overgrown habitats the geometric distinctiveness of the pattern may therefore serve to catch the eye at the earliest moment possible and signal the presence of a conspecific, allowing an approach or a retreat without having to come within fighting distance. (This of course depends upon the pattern being restricted to one species throughout that animal's range and it may be significant that there is no natural overlap of range between *Civettictis*, *Nyctereutes* and *Procyon*.)

While the civet can normally rely on slinking quietly out of sight to escape from enemies, it may jink about as it gallops into deeper cover. It can double its size by raising the crest of long hairs down its back and tail and fluffing out its long shaggy hair. If cornered, it gives extraordinarily deep growls and an explosive cough, and the combined magnification of impact in an otherwise rather insignificant animal has been seen to intimidate attacking dogs on more than one occasion. Presumably the erection of fur and crests can be equally well employed to impress rival civets.

While the nape of the civet's neck is also crested with grizzled grey fur it has white sides and a black throat. The white streaks are generally heavily outlined in black and Ewer has suggested that they may have the function of orienting bites to a region where there are no vital structures near the surface since she saw fighting civets bite predominantly at this area. Perhaps it is the peering, painted face in the dark, the deliberate rather ritualistic movements and an amorphous plasticity of form achieved by the mobile crest that have earned the civet its Swazi name of "he who puzzles the spirits". I have tried to put forward functional explanations for some

peculiarities of external form and behaviour that disguise an otherwise generalized mammal but in many respects the civet remains an enigma both to spirits and scientists.

The adaptability of the species is expressed in a very wide range in Africa and in the occupation of numerous habitats. They are abundant in lowland and montane forests and in the mosaic of cultivation, fallow, marsh and forest that covers much of Uganda, they can live in grassy savannas, reed beds and canebreaks of elephant grass, *Pennisetum*, but need a ready refuge as the grass is regularly burnt off. Likewise, they will occur within areas of open or arid country where there are thickets or dense scrub along drainage lines or on rocky outcrops. They are absent from the arid parts of Africa, The Sahara, Somalia and South-west Africa and it is probably the openness of the habitat that is as important as the aridity. While they seem capable of subsisting for a while in waterless areas, they are probably dependent on moist foods.

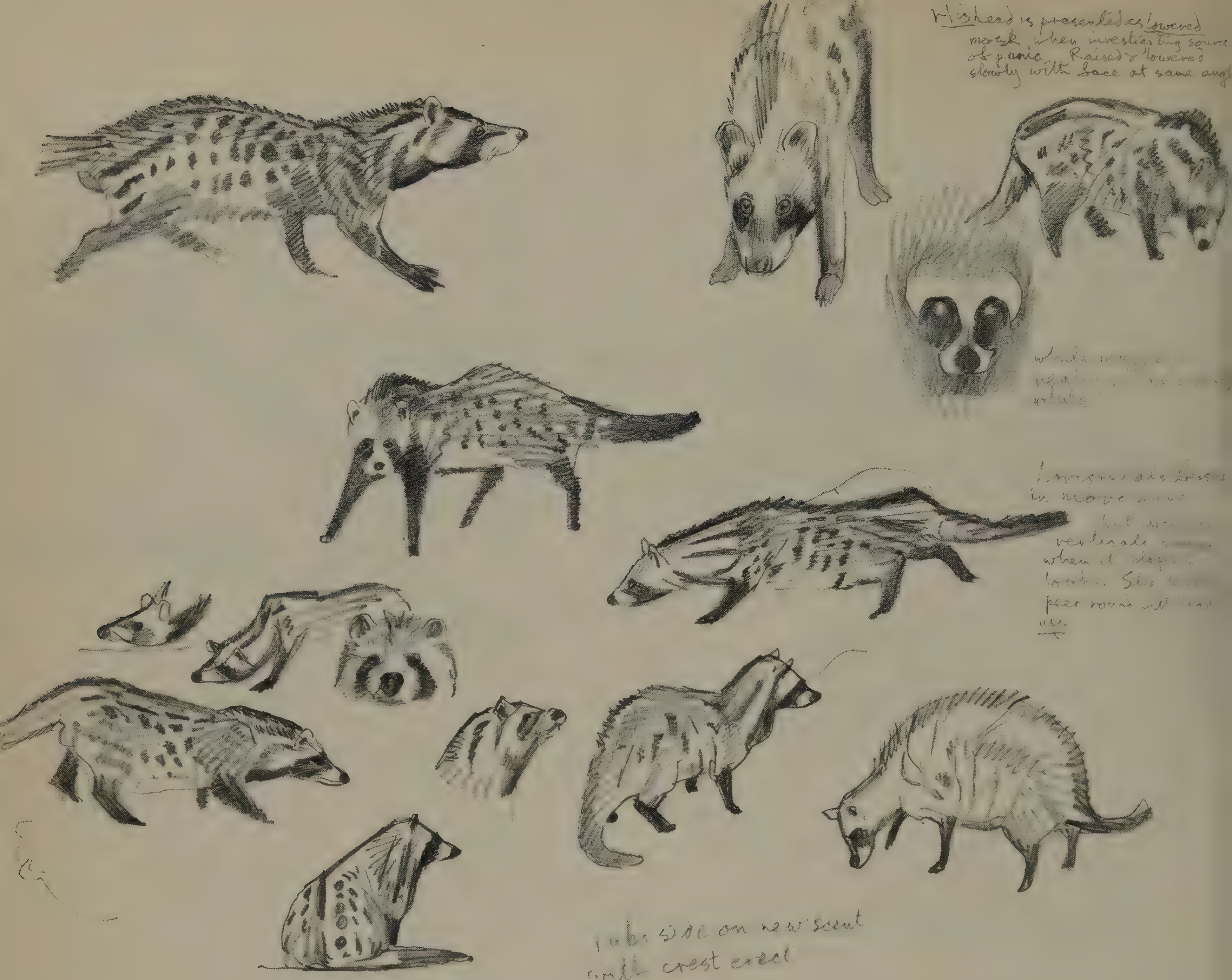
Civets take readily to water, swim well and co-exist with *Atilax* in some extensive marshy areas. They are absent, however, from Pemba and Mafia Islands although present on Zanzibar. The last island is known to have been a centre for the trade in civet so introduction from the mainland should not be discounted. In Lake Victoria, one island, Fumwe, is named after them and as the only carnivorous land mammal there, they were said to have been particularly numerous at one time.

The range of recorded foods is truly astonishing. They feed on many sorts of insects, including the stink grasshopper, *Zonoceras elegans*, dung beetles, larvae, fly maggots, cockroaches and termites. Other invertebrate foods include myriapods, snails and crabs. They eat tortoises, snakes and lizards, frogs and stranded fish. They will feed on carrion of any sort and commonly scavenge offal of all kinds around villages. They have been seen to catch and kill ground-dwelling birds and to eat their eggs and those of reptiles, and they may kill various small mammals if they have a chance. A hare, *Lepus*, and a banded mongoose, *Mungos*, have been seen being killed by civets. They will also subsist entirely on vegetable food including grass, leaves, growing shoots and the fibre of succulents, roots and ground crops such as sweet potatoes and peanuts are dug up and eaten. Almost any type of fallen fruit is eaten, including the normally rather poisonous *Strychnos* spp. The fruit diet is most conspicuous in forest and thicket habitats where an examination of dung shows that they may feed on little else for long periods. Cultivated gardens especially papaya and maize plantations are raided and they fell maize plants to reach the cobs. Once a steady source of food has been found the civet will return regularly, whether the source is a house or village midden or a fruiting tree. Fruit is simply sniffed at and eaten, pips, stones and all with minimal chewing. Bony carrion such as chicken legs may be broken up by rapid champing of the molars but is then swallowed whole. Eggs are taken in the mouth and tossed sideways to break

them. Living prey is approached cautiously, snapped and dropped or given a violent toss after being bitten. Prey that might bite is seized, given a very vigorous shake and then dropped or tossed with a leap. Ewer (1973) noticed that there was no direct neck bite and she suggested that the violent shaking usually served both to dislocate the vertebrae and disable the prey from retaliating. She thought this compensation for the lack of accuracy and the civet's evasive leap might be adaptations for coping with snakes.

While many of the approach movements are cautious or deliberate, the civet's feeding is rather rapid with powerful but perfunctory chewing. The amount eaten is large and an adult can eat nearly two kilos in the course of a night. In spite of this, it is said to be able to go without food for a fortnight and Bothma (1965) noted that a stomach retained some rodent teeth in it which had obviously been eaten long before the civet was killed. Coping as it seems to, with near poisonous or at least very distasteful foods, and including the coarsest types of vegetable and animal fibres in its diet, the civet's digestive system is probably somewhat unusual.

Civets only feed and are active at night, although they are occasionally seen about in the evening or early morning on overcast days. Ewer (1973) noticed that both sexes move about much more while sexually active and



this might affect both activity periods and the area within which an animal ranges. The diurnal shelter is probably only stable for a female while she has cubs but even this lair is readily changed if the litter is disturbed. While civets often sleep in termitaries or rock crevices, such secure shelters do not seem to be a necessity and they are often put up from temporary lairs where they may be scarcely protected from the rain.

Civets prefer to use habitual pathways and they establish dung middens on some open patch of relatively dry or sandy soil. As such sites are often chosen by neotragine antelopes or kongoni for their dung, it is not uncommon to find civet dung and antelope droppings accumulated together.

Apparently only one civet uses a deposit-site and it is not closely associated with scent marking. It seems likely that only one dung deposit is used at a time and that it is near the centre of an individual's home range, whereas the scent deposits are more evenly distributed around, particularly at the junction of pathways (Rahm, 1966). One deposit I passed from time to time was on a forest road in western Uganda. Although the exact location was occasionally moved a few metres up or down the road the same general area was used for at least five years.

Rahm has stated (presumably on the strength of their conspicuous dung deposits and scent smears), that civets occupy well defined territories. On a flat surface the scent smears may be visible as separate marks, each with the clear outline of the gland's margin, but it is not known to what extent male—female and adjacent ranges overlap, although sexual activity must demand changes or extensions of range.

Birth records from East Africa are scattered but, as strongly seasonal breeding patterns have been reported from Zambia (Ansell, 1960b), South Africa and a European zoo (Mallinson, 1973), the possibility of birth peaks should be looked out for in this region. Captives are known to be capable of producing three litters a year. Presumably an oestrous female advertises her condition through the scent of her urine and through her scent glands. As in several other carnivores, there is a difference between male and female in the direction urine is projected, the male spraying back, the female downwards.

There have been no suggestions as to what factors influence the timing of sexual behaviour, but it was the male of a captive pair that gave Ewer (1973) a portent of subsequent sexual behaviour by its increased activity and a tendency to trot about with mouth slightly open. Males also make a lip-curling gesture. The female at first avoids the male's advances or she may snap at him. The male withdraws or appeases with a characteristic gesture of submission, laying its head and forequarters down on one side thus exposing the side of the neck, which is generally given a symbolic bite by the female. Mating is invariably preceded and followed by female attacks and, from a variety of observations on captives, it appears that females are dominant over males. The male of one pair kept by Alan Root was so persistently attacked that he lost a lot of his fur before he was separated.

Although Ewer did not see any response on the part of the female, the courting male was heard to employ a clucking cry which is otherwise restricted to juveniles keeping in contact with one another or with the mother and is used by the mother to call the young. As for the male, the progress of the female's oestrus is betrayed by increased activity and scent marking and eventually the female appears to incite a chase by running close past the male, which provokes him to pursue her until she sinks to the ground and then he mounts her, laying his head along her neck but not biting her. This token submission by the female lasts less than a minute, an unusually brief copulation for a carnivore; the female may miaow at intromission and usually turns on the male again immediately after mating. Although some captive pairs will live together without excessive conflict, in the wild bonds are unlikely to be maintained beyond the courtship period.

Gestation lasts 60—72 days and a litter of one to four young are born in a hole, hollow trunk or termitary. They open their eyes anywhere within a few hours up to four days from birth and grow very fast. Verheyen (1951) says they stay in the shelter just over a week. If frightened or disturbed they make a very snake-like hiss and sharp spitting noises. Ewer has pointed out the combination of dog-like tugging followed by cat-like treading at the teats and she observed that each civet cub used its own teat. Because the members of the litter become more aggressive towards one another as they grow up, the elimination of competition for milk may be important. Nonetheless, the young keep in touch with one another with a clucking cry and become distressed if lost. As they mature, this call is used less and less until they become as silent as the solitary adults. It has already been mentioned that the call makes its reappearance in the male's courtship and the cubs come to the mother's clucks but only when they are very young does she reply to their calls herself.

Weaning begins at one month and the young lick the mother's mouth at this age. Captive mothers continue to produce milk for 15—20 months. In some litters females grow more rapidly than males.

Whether the young are driven off by the mother or disperse of their own volition is not known but I have examined over twenty civets run over on roads and only in two instances were the animals fully adult. A high proportion of road casualties occurs where roads pass between high cut banks. The civet tends to be dazzled and stares owlishly at an oncoming car; it only flees at the last minute and then jinks wildly from side to side. Why are

subadults more vulnerable on the roads? Do they need to search more widely and for a longer period for their food? Is there a general propensity for civets to follow tracks before the animal has established its own home range pathways; is this age group forced to wander because of the exclusion from adult ranges, or are they simply less cautious? The answers await further study of the natural history of this interesting and common species.

Cars are probably a lesser danger to civets than hunters with dogs, nets, traps, for all of which the civet is a ready quarry. In many areas civets are hunted for their excellent white meat or in retaliation for raiding hen coops and gardens but in more tolerant localities they are licit and familiar household scavengers.

Although some dogs are intimidated by the civet's displays, the larger breeds are generally less impressed and are more impervious to the civet's bites. (It should be remarked that the civet, unlike many other viverrids and mustelids, does not emit secretion from its glands when it is alarmed and their scent is not nauseating as suggested by Dorst and Dandelot, 1970.)

Apart from man and his dogs, the civet probably has few predators. One has been recorded killed by a lion and leopards may take them occasionally. Their very varied sources of food are competed for by numerous other animals, of which mongooses, the sidestriped jackal, *Canis adustus*, and the bush pig, *Potamochoerus*, are among the commonest and most likely to come into contact with them.

Nothing has been published about the diseases to which they might be prone. They are popular zoo animals, being easy to feed and keep and they have been known to live fifteen years.

Viverricula indica

Indian Civet (Viverricula indica)

This Oriental species was introduced to Pemba, Zanzibar and Mafia Islands at an early date. On Zanzibar it co-exists with the African civet, *C. civetta*.

Palm Civets
Paradoxurinae

This primarily Oriental group is represented in Africa by a single species, *Nandinia*. Although specialized species occur in the Far East, the African palm civet is a typical member of the subfamily.

Palm Civet (Nandinia binotata)

Family Viverridae
Order Carnivora
Local names
Miyayu (Luganda), Cupita (Kuamba, Lubwizi), Imbukula (Kikinga, Kinyakyusa), Imbuli (Kinyika), Mowe (Sebei), Liwala (Lugisu), Ninamugogo (Ragoli), Kunamugogo (Lutereki), Mbala (Lukiga)

Measurements
head and body
51 (45—58) cm
tail
58 (50—62) cm
weight
2 (1·70—2·1) kg

Palm Civet (Nandinia binotata)

Nandinia binotata

Unlike genets, *Nandinia* is a very inconspicuous animal and its blotching and mottling are well adapted to allow it to blend with the rough bark of trees and the shadows cast by leaves. Even the yellow-green eyes are a camouflage during daylight since the pupil closes to a vertical hairline. If disturbed during the day, *Nandinia* generally makes rather lethargic, deliberate movements which have led observers to describe it as slow-moving. This behaviour is a strategy to enhance its cryptic appearance, for it is capable of running along the branches at great speed at night.

The tail, which is generally of the same length as or longer than the body, is exceptionally well muscled and sturdy. Although not actually used to grip branches, it is employed as a brace in difficult manoeuvres when the forepaws are used for prey. It serves as a balancing rod on thin branches while its stiff flailing movements may help create more resistance when the animal leaps to the ground.

The toes are armed with retractable claws and the inner digits of the forepaws are somewhat divergent to form clawed "thumbs". All four limbs are exceptionally powerful with their highly flexible joints bound around with thick sheets of connective tissue. The toes and palms of the feet have pink naked pads and an area of very thick skin with a peculiar pattern made by deep cracks extends back along the lower surface of the tarsus. This area of skin can be seen to function as a friction pad whenever the hindlimbs take the weight of the body. The palms exude a sebaceous secretion, the scent of which is no doubt detectable to other palm civets.

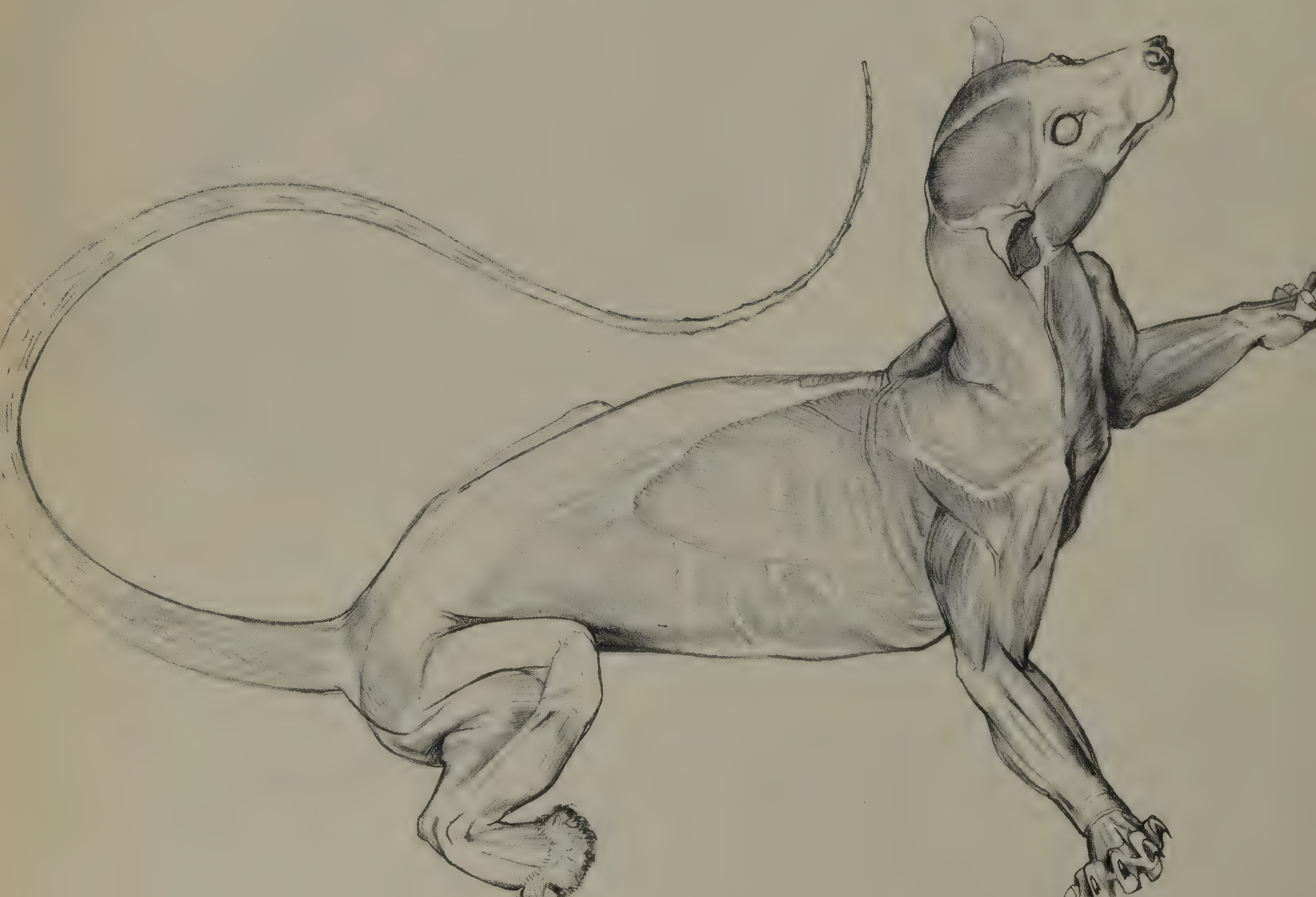
This is only one of the numerous smells and secretions produced by this species. Between the third and fourth toes of each foot there is a glandular pocket which is overlain by a patch of yellow fur. This can presumably scent the trail and particularly scratch-marks on bark. Along the midline of the lower abdomen, in front of the genitalia of both sexes there is a narrow slit which can open up to reveal an extensive area of naked glandular skin which produces a strong-scented brown secretion, which can be deposited by the animal simply opening the pocket and rubbing its belly on the branch. I have also noticed a male's tendency to rub its chin on branches. This action might pick up secretions already on a bough but it seems more likely to be a means of depositing scent, possibly salivary in origin or emanating from chin glands invisible to the naked eye. Another secretion appears to be restricted to lactating females and might be produced by the skin overlaying the mammary glands. It stains the fur of the belly in a lactating female a brilliant orange-yellow and rubs off on to the young. Both sexes have a musky smell and a slightly greasy underfur, which may imply the presence of scent producing cells that are more generally distributed over the surface of the body.

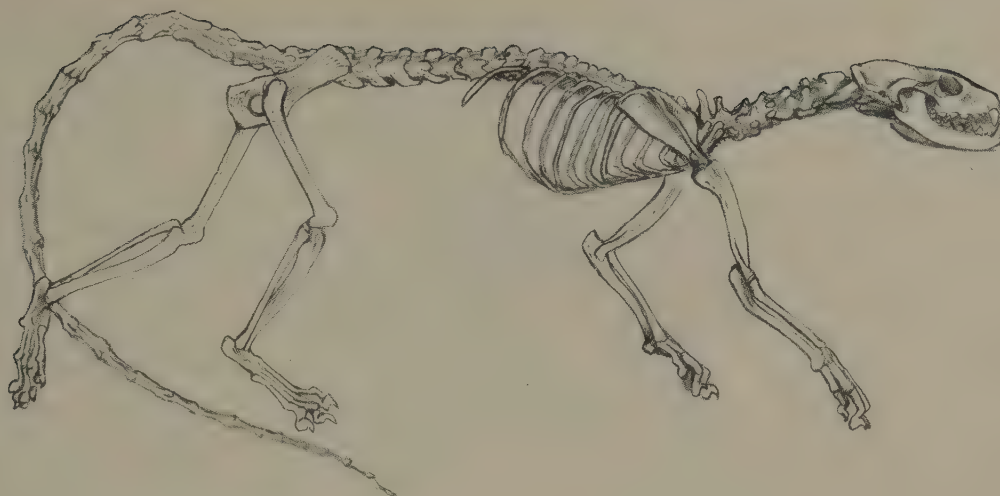
Like any other species, *Nandinia* can also have the usual tokens of dung, urine and perhaps anal and vaginal secretions to augment its battery of scents. Like the Prosimians, *Nandinia* leaves a scented trail along the boughs, trunks and ground over which it travels and captives scent particular landmarks in their cages with their ventral gland. It seems likely that the suppression of

all visual signals in favour of a cryptic appearance may be compensated to some extent by the elaboration of the olfactory communication system. Special secretions, such as the yellow stain associated with lactation, may convey information about the sex and status of individuals which allows certain social interactions to be avoided or regulated without the need for any direct meeting or visual signals taking place.

Nandinia's coarse, cryptically coloured coat with its thick woolly underfur, may be adapted to an existence that is at least partially nomadic. Solitary individuals have been seen remaining in a single tree for the duration of its fruiting period, sleeping curled up in a fork or in a tangle of thick foliage and looking like a large knot or gall in the bark or a wasps' nest. If the animal has emancipated itself from the need for a secure and sheltered home base a warm and weather-proof coat and camouflage are obvious advantages. The latter may be as much an insurance against harassment by the birds, squirrels and monkeys that crowd into fruiting trees during the day as it is a protection against potential predators such as hawk eagles, leopards or pythons.

In spite of being predominantly nocturnal, *Nandinia*, may attack birds and monkeys but it would be early or late comers and roosting sleeping



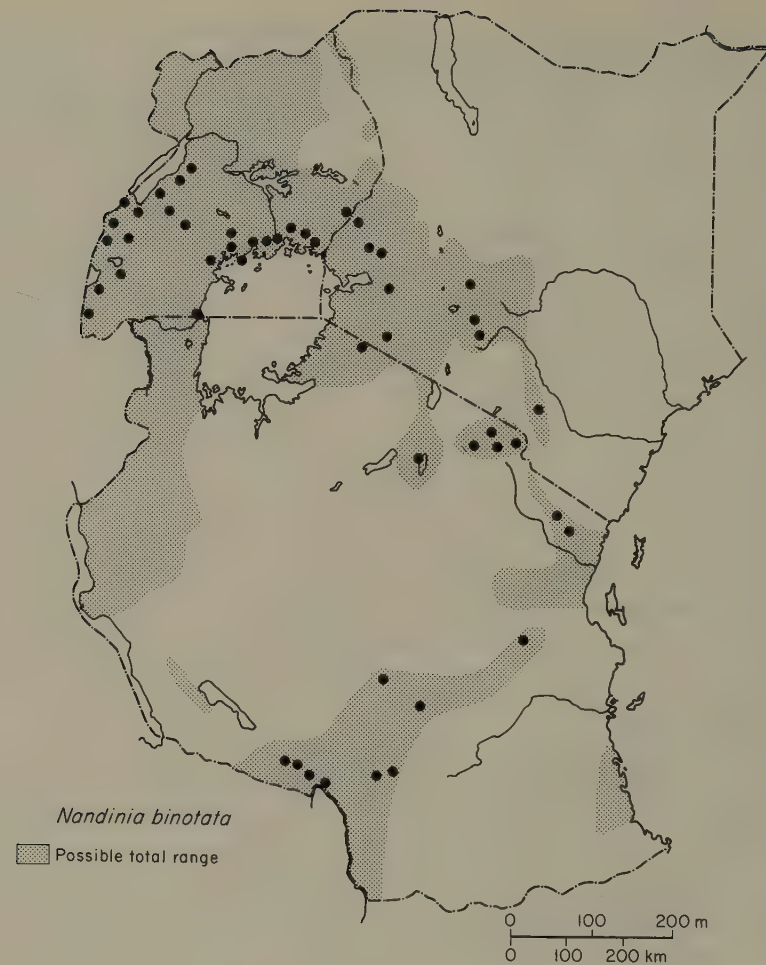


individuals that would be the most ready prey. Fruit bats, which are often attracted to fruiting trees in great numbers, have also been reported in their diet. Ewer (1973) reported a captive attacking a half grown Mona monkey as well as killing a Potto.

While *Nandinia* has truly omnivorous tastes it does not hunt prey such as adult birds and mammals when they are active. Instead it visits roosts and hen yards and can kill birds as large as a turkey. Rodents, insects, eggs, carrion, pineapples and fallen fruit are caught or foraged for on the ground and it is commonly seen or trapped at ground level, and sometimes prefers to run down or leap out of a tree in alarm rather than run through the canopy. The Asiatic palm civets are often called "toddy cats" and captive *Nandinia* are also reported to show a weakness for alcohol which may originate in their eating fermenting fallen fruit and tree exudates. *Nandinia* will travel some way out of the forest in search of food and I have collected a lactating female beside an enclosed courtyard where a colony of masked weaver birds, *Ploceus*, was nesting. The nearest patch of forest was one kilometre away and the palm civet had crossed open fields and climbed walls to reach the courtyard, where she had managed to extract eight weaver-bird fledglings from their nests. She had not killed any adult birds but her feat of climbing down thin branches resembles that reported by Bates (1905) who had a drying chimpanzee skull gnawed by a palm civet that had travelled down the string by which it was suspended.

The majority of records show that fruit is the commonest food, notably *Ficus* spp., *Musanga cecropoides*, *Myrianthus holstii*, *Uapaca* and the pulp of *Elaeis* nuts and cultivated fruit such as bananas, pawpaws and passionfruit. Rahm and Christiaensen (1963) retrieved leaves of *Galinsoga parvifolium* and the fern *Pteridium equilinum* from stomachs in the Kivu area.

Nandinia will feed at any level in the forest from the top canopy to the ground. They hold their food with the forepaws and in the branches they will twist their hindfeet about in a variety of positions in order to get a stable base with these two limbs and thus release the forearms to manipulate food; the divergent inner claw and the breadth of the paw allow a firm grip. Living



prey is held fast and killed with a series of extremely fast and penetrating bites; small mammals and birds are swallowed almost whole and there is no tossing or shaking which could waste or lose food or upset the predator's grip.

If a palm civet should fall it is unlikely to sustain damage, for it is capable of jumping out of tall trees voluntarily. In fact, Thorneycroft (1958) saw a *Nandinia* drop down with its tail and legs spreadeagled only to climb the tree and repeat it again as if it were a game.

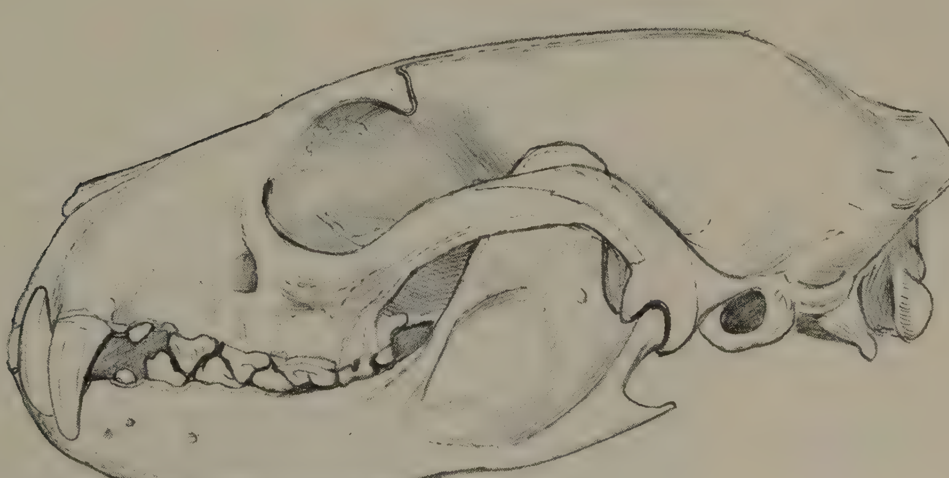
Such a facility in leaping down could also serve as a means of breaking off any unwanted contact. *Nandinia* is predominantly solitary but the young accompany the mother very closely until they are approaching adult size and I have one record of a near adult male accompanied by a juvenile male which could not have belonged to the same litter. Adult male and female pairs have been seen together but this is unlikely to be a lasting association and a mother with young has not been reported in the company of an adult male nor have I any records of lactating females that were simultaneously pregnant, although I have seen *Nandinia* of varying sizes within a relatively small area where there was a localized fruiting of *Musanga cecropoides*. While these trees were in fruit they attracted at least 12 or 15 *Nandinia* into less than a kilometre of forested valley; they were likely to have come from a larger catchment area as no animals were seen after the season was over. The

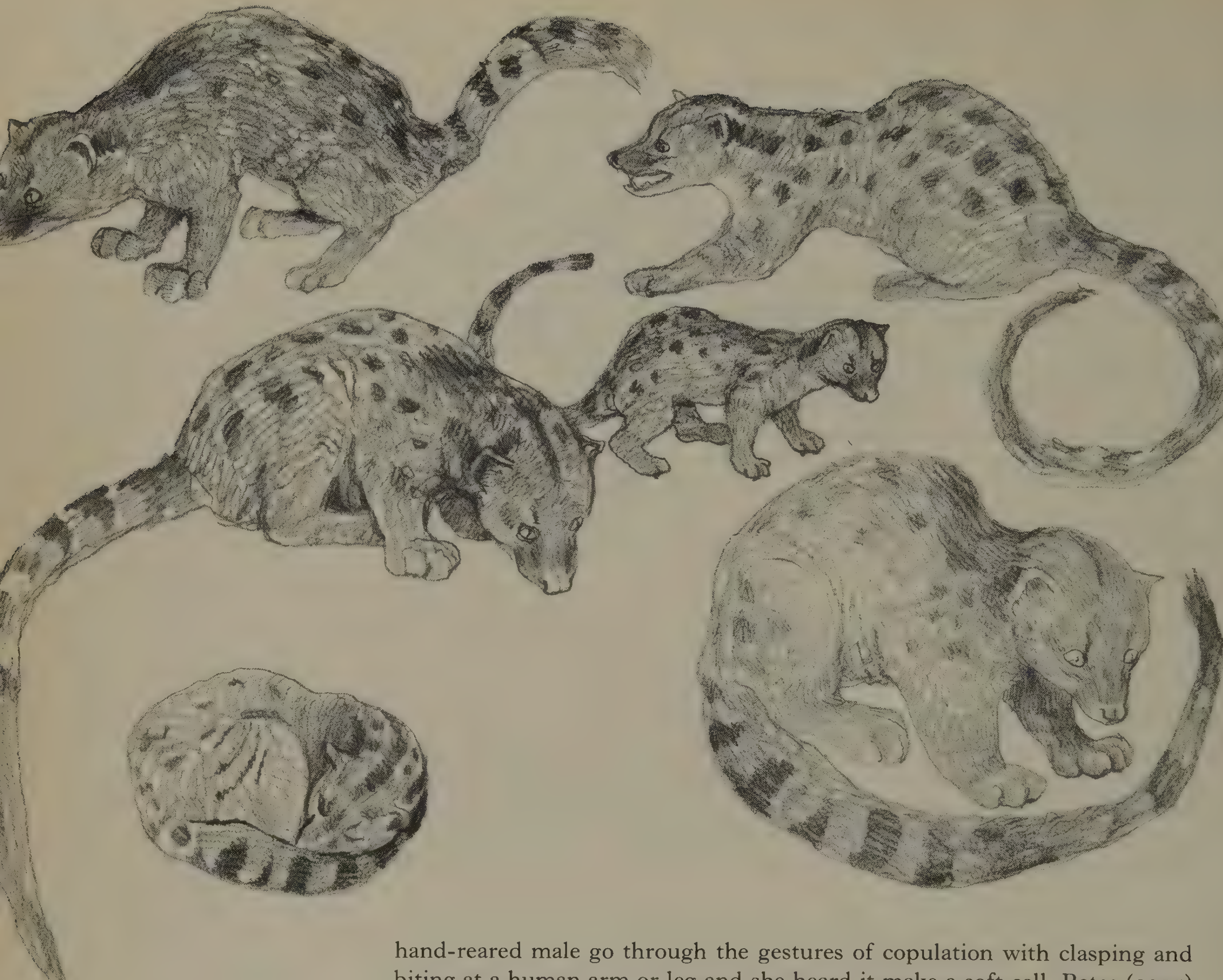
animals were well spaced but it is possible that several individuals visited one tree in the course of a night. A farmer on the edge of the Kaimosi Forest had his poultry persistently attacked by palm civets. Even after nine animals had been trapped sporadic visits continued and there seems little doubt that *Nandinia* are numerous in forest and that they may be fairly nomadic.

I have twice seen a mother feeding on fruit with her two young and have heard a miaowing contact call. Vosseler (1928) had a tame and possibly imprinted *Nandinia* that called when shut up but, when allowed to come into contact with its keeper, it changed to a deeper note accompanied by much sniffing. This animal played like a cat with a human hand but always kept its claws sheathed. Vosseler noted, however that if he administered a smack it behaved much more like a submissive dog, lowering its body, particularly the head and remaining in a subordinate position, meanwhile following its keeper with its eyes. Perhaps Vosseler had unwittingly assumed the role of rejecting mother or of dominant neighbour while the young captive showed appeasement in a posture that might inhibit further attack and would incidentally display the only non-cryptic markings, two white shoulder spots after which the species is named.

Nandinia are active from dusk for about four hours, after which time sightings are rare in the wild while captives tend to sleep for some hours. A further few hours of activity precede dawn during which captives like to race around.

Vosseler (1928) reported breeding taking place at Amani between July and August. Ewer (1973) reports them breeding twice a year and eight Uganda records of lactating females or young suggest that there may be two birth peaks or seasons, one in May the other in October. Both these months are wet following the annual rain fall peaks and they are followed by relatively dry periods. Mating has not been described but Ewer (1973) watched a solitary



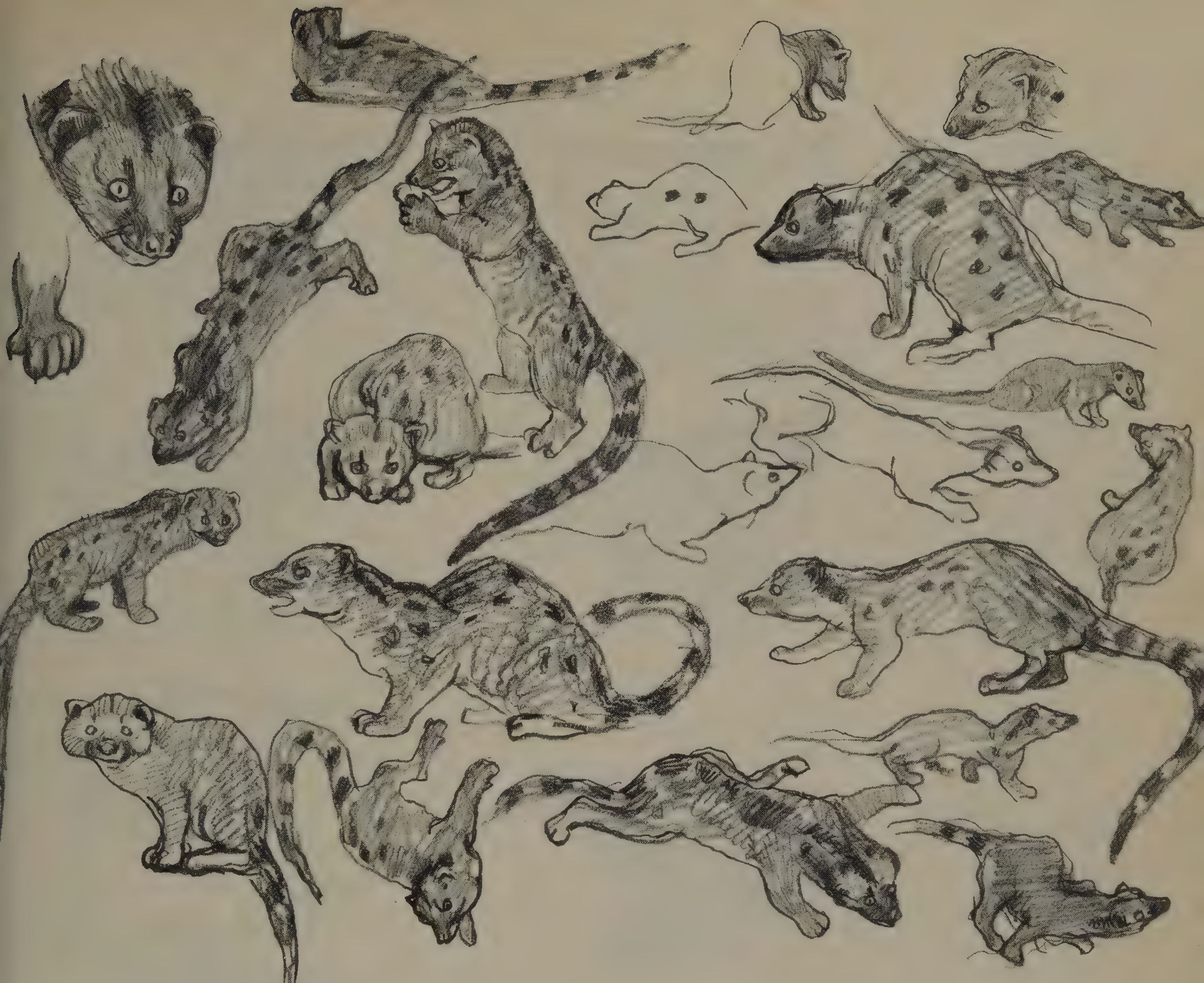


hand-reared male go through the gestures of copulation with clasping and biting at a human arm or leg and she heard it make a soft call. Bates (1905) also heard two animals calling to one another with a faint mew.

Up to four young are born but the normal number is two. The female appears to produce milk from as many teats as there are young which suggests that each kitten uses a single nipple exclusively.

Having seen the dorsal fur of two partly-grown *Nandinia* stained with the bright orange secretion from the mother's belly I did think at one time they had been marked with the ventral gland (Vol. I, p. 289) but further investigation has suggested that this secretion might have an exclusive association with the lactating mother and by contagion, her young. Since mating appears to be avoided during this period it is possible this might be a device to repel sexual approaches by males or neutralize attacks on the young. If the males are continuously sexed, the timing of the female's oestrus might be co-ordinated with an absence of orange secretion, but this remains to be shown.

The young are born after a 64-day gestation in some arboreal shelter such as a hollow branch but they soon accompany the mother and weaning probably starts at an early age. The young purr like kittens when sucking.



Vosseler described a captive as quarter grown at two months and he remarked that this animal was most active and went through the most intense learning phase between the age of three to five months, which would coincide with the period of mother care in the wild. This captive learnt to raise a bar on a cage, would indulge in sudden bursts of noisy rushing about, would tear up material, made a loud howl if its tail was accidentally hurt and, like other captives and most viverrids used a single latrine.

Animals are fully grown and are sexually mature at one year (Michaelis, 1972). As they are omnivorous, their diet overlaps that of many other animals, but other species either do not eat such a diversity of foods or cannot range through all the layers and vegetation types of the forest and its edges. Potential predators have been mentioned and disease might be a factor controlling populations. I collected one specimen that had a very perforated liver but was otherwise healthy.

They used to be hunted and eaten in Bugisu and they are commonly trapped raiding chicken coops. The species is common in most forested areas of East Africa and deserves more study than it has received to date.

Mongooses

KEY TO MONGOOSE GENERA

Herpestinae

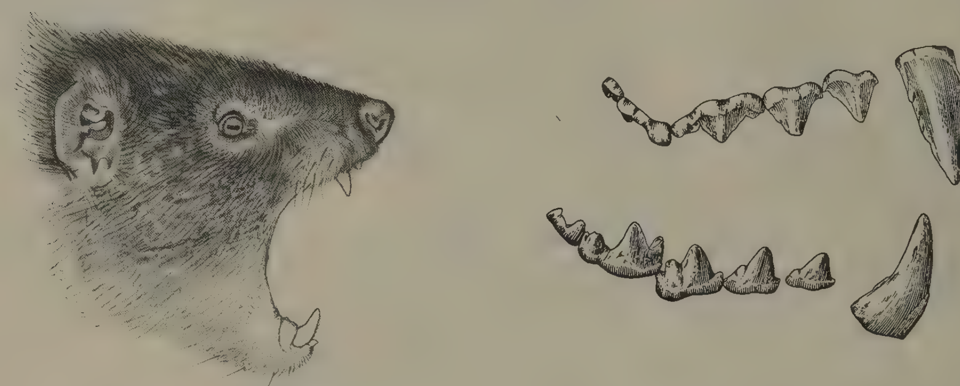
The viverrids are generally typified by reference to the Herpestine mongooses and the subfamily has been discussed in the viverrid profile. Primarily terrestrial they are never blotched or spotted and coats are normally grizzled and coarse in texture. See Ewer (1973), Rosevear (1974) and Pocock (1916c) for detailed diagnoses.

Tooth Formula

Atilax

$\frac{3.1.3.2}{3.1.3.2} = 36$

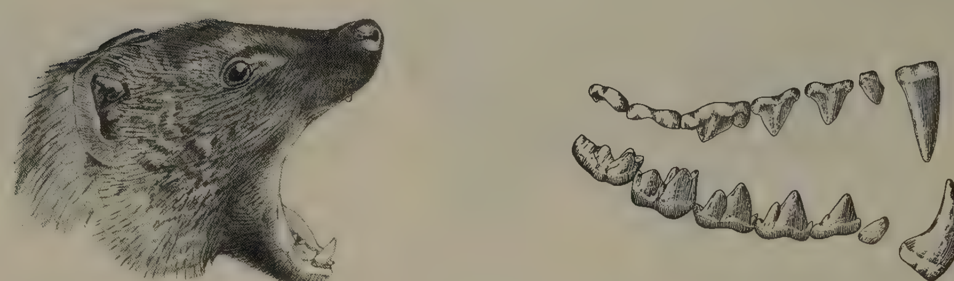
Profile on p. 207



Icheumia

$\frac{3.1.4.2}{3.1.4.2} = 40$

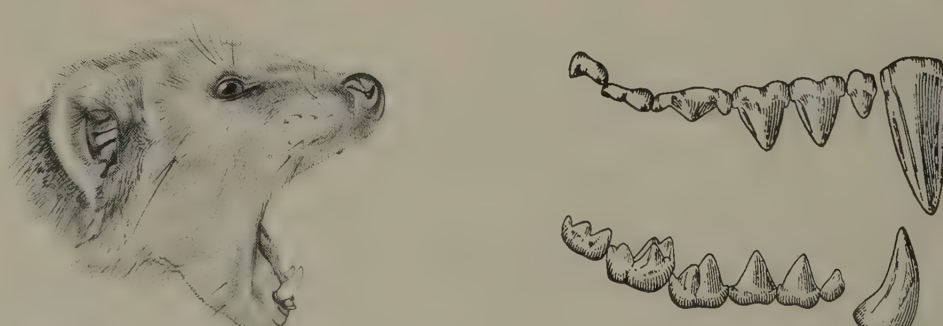
Profile on p. 233



Bdeogale

$\frac{3.1.4.2}{3.1.4.2} = 40$

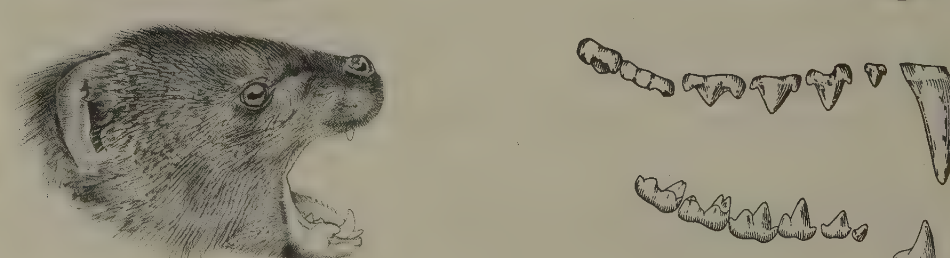
Profile on p. 243



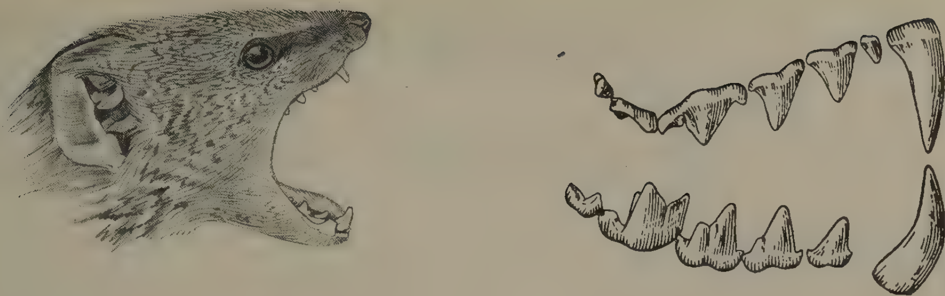
Rhynchogale

$\frac{3.1.4.2}{3.1.4.2} = 40$

Profile on p. 239



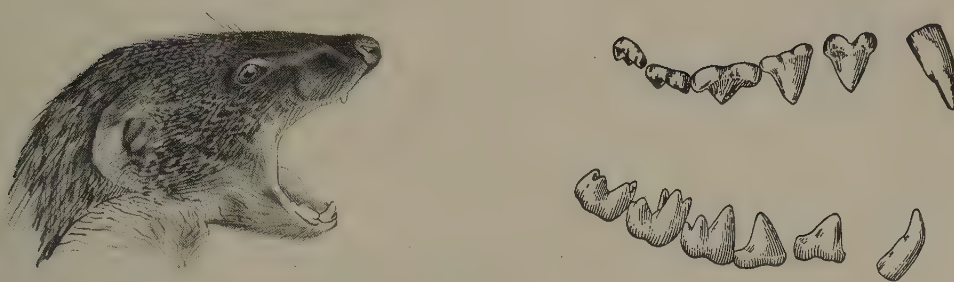
Tooth Formula



Herpestes

$\frac{3.1.4.2}{3.1.(3\text{–}4).2} = 38\text{–}40$

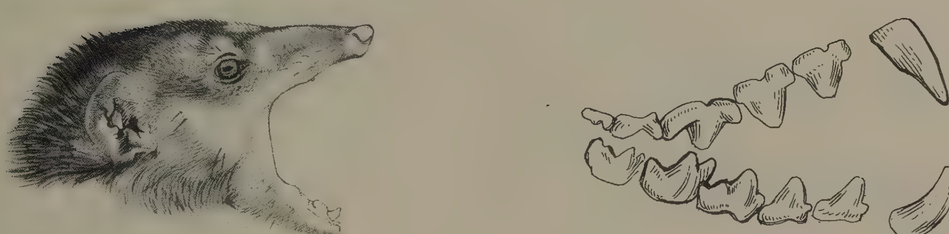
Profile on p. 179



Mungos

$\frac{3.1.3.2}{3.1.3.2} = 36$

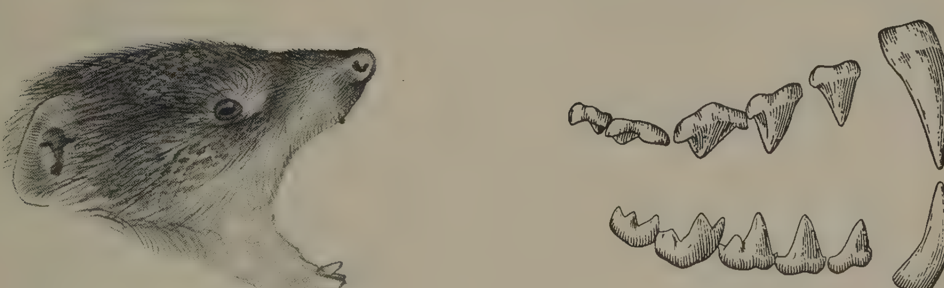
Profile on p. 215



Crossarchus

$\frac{3.1.3.2}{3.1.3.2} = 36$

Profile on p. 227



Dologale

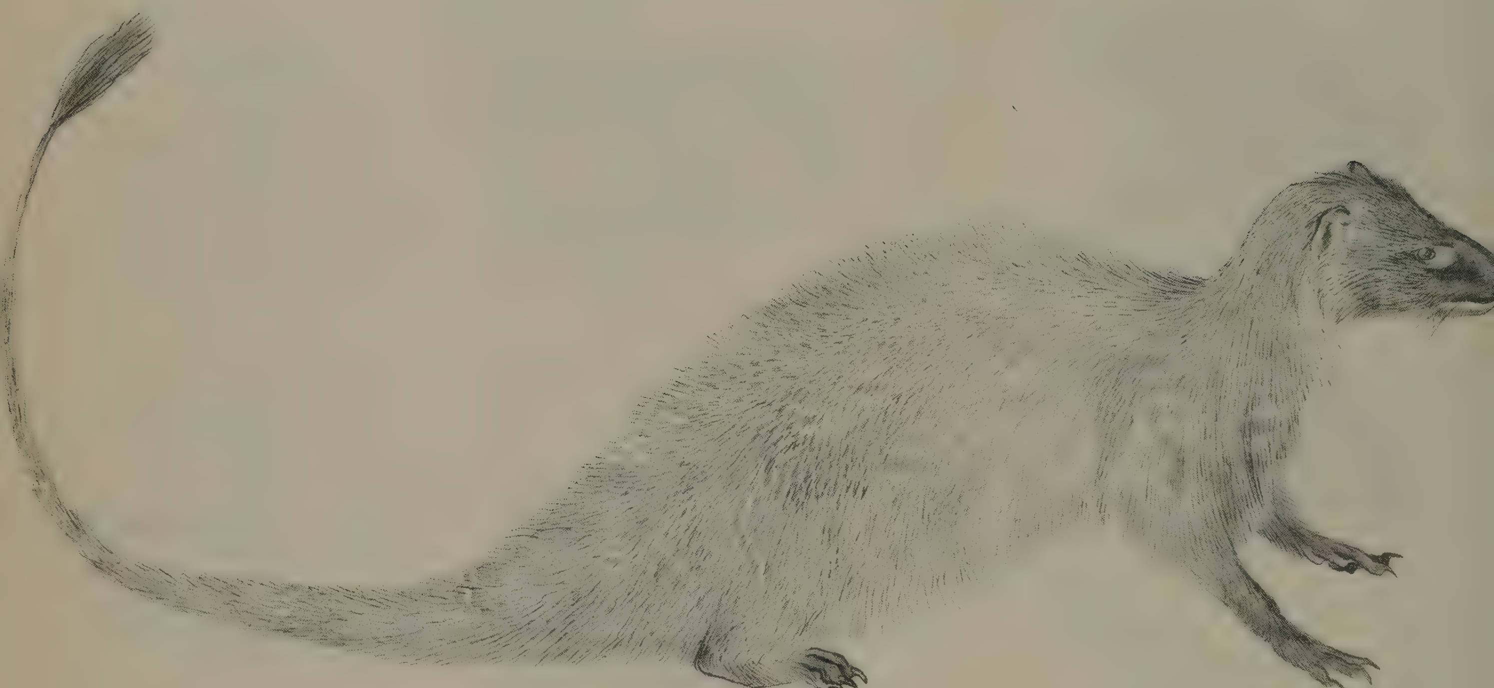
$\frac{3.1.3.2}{3.1.3.2} = 36$

Profile on p. 205

Helogale

$\frac{3.1.3.2}{3.1.3.2} = 36$

Profile on p. 193



Ichneumon, Egyptian Mongoose (Herpestes ichneumon)

Family Viverridae
Order Carnivora
Local names
Nyeretzi (Kikinga), Ekosemate (Karamojong), Okak (Lwo), Churunguru (Sebei), Serengeta (Lugisu), Anamambi (Kitosh), Mogoeet (Masai), Lunamakeki (Kiragoli), Ewori-wori (Ateso)

Measurements
head and body
48—60 cm
hindfoot
9—9·8 cm
tail
33—54 cm
weight
1·7—4 kg

Ichneumon, Egyptian Mongoose (Herpestes ichneumon)

Herpestes ichneumon

Very widely distributed over the African savannas, this species is a familiar sight as it crosses roads in heavily grassed or cultivated areas. Its very long, low-slung form often presents a remarkably reptilian silhouette when seen from a distance; this is due partly to the gliding gait and smoothly tapered tail and partly to the legs being hidden by a hanging fringe of body fur. The coat is a grizzled grey with a conspicuous black tassel on the tip of the tail. As with several other species of carnivores, the overall colour and tone have some correlation with humidity.

The snake-like appearance is even more pronounced when several animals follow one another, at which time each animal tends to raise its tail and keep its nose close to the genital area of the one in front. This use of scent-following, augmented perhaps by a visual marker in the black tassel, is well suited to a species living in long grass but also has a bearing on other peculiarities of the species. The behaviour seems to originate in the young following the mother while they are still relatively small and the scent gland presumably acts as an adhesive device in a similar manner to the tail clutching of baby shrews. It is a frequent observation that glandular secretions enhance an animal's confidence and both marking and sniffing behaviour are precipitated by strange surroundings in a wide variety of species, including *H. ichneumon*. The anal gland following could, therefore, serve several important functions simultaneously. First there is the retention of contact along narrow tunnels through dense grass; secondly the strangeness of the environment may be counteracted for the young by familiar scent; finally, there is the scare value against predators.

These last two factors are well illustrated by a hunter's encounter with what he called "a dragon biting its tail" and turning round in endless circles: he had surprised five baby ichneumons, the mother having fled at his approach. Each infant was following its sibling, its vision obscured by an overhanging tail, so that they formed a complete circle, all running on blindly as fast as their legs could carry them. As the hunter came nearer, the little animals suddenly broke loose and in the observer's words dashed off "like a snake that had cut itself into pieces, each with a separate existence" (De La Fuente, 1972).

There is yet another facet to this behaviour; the urge to chase an anal gland is often so strong that an individual, in the absence of a fellow, will try persistently to put its nose under its own tail. It is one of my earliest memories seeing an ichneumon chasing its own tail on the lawn of our garden and my astonishment at the time was apparently shared by a collection of bulbuls, sparrows and sunbirds, which landed on the grass and nearby bushes to scold and mob the contortionist. Suddenly the mongoose made a dash at a bird and, although it missed, there was no doubt about its intention. Other observers have seen a successful outcome to this play. Preston (1950) saw a mongoose kill four guineafowls after adopting various contortions,

Hepestes ichneumon

rearing up and falling from side to side, and Pitman (1931) described them "rolling nearer, ever nearer to their prey".

The subadult individual illustrated in this profile was captured with a coat, thrown over it while it was utterly engrossed in chasing its own tail, and I suspect that once, while driving across a tussocky promontory in Kabalega Park, I interrupted a large adult engaged in this same performance. A party of agitated guineafowls caught my eye and on approaching a mongoose broke cover and started to move unhurriedly away, hotly pursued by seven or eight scolding guineafowls.

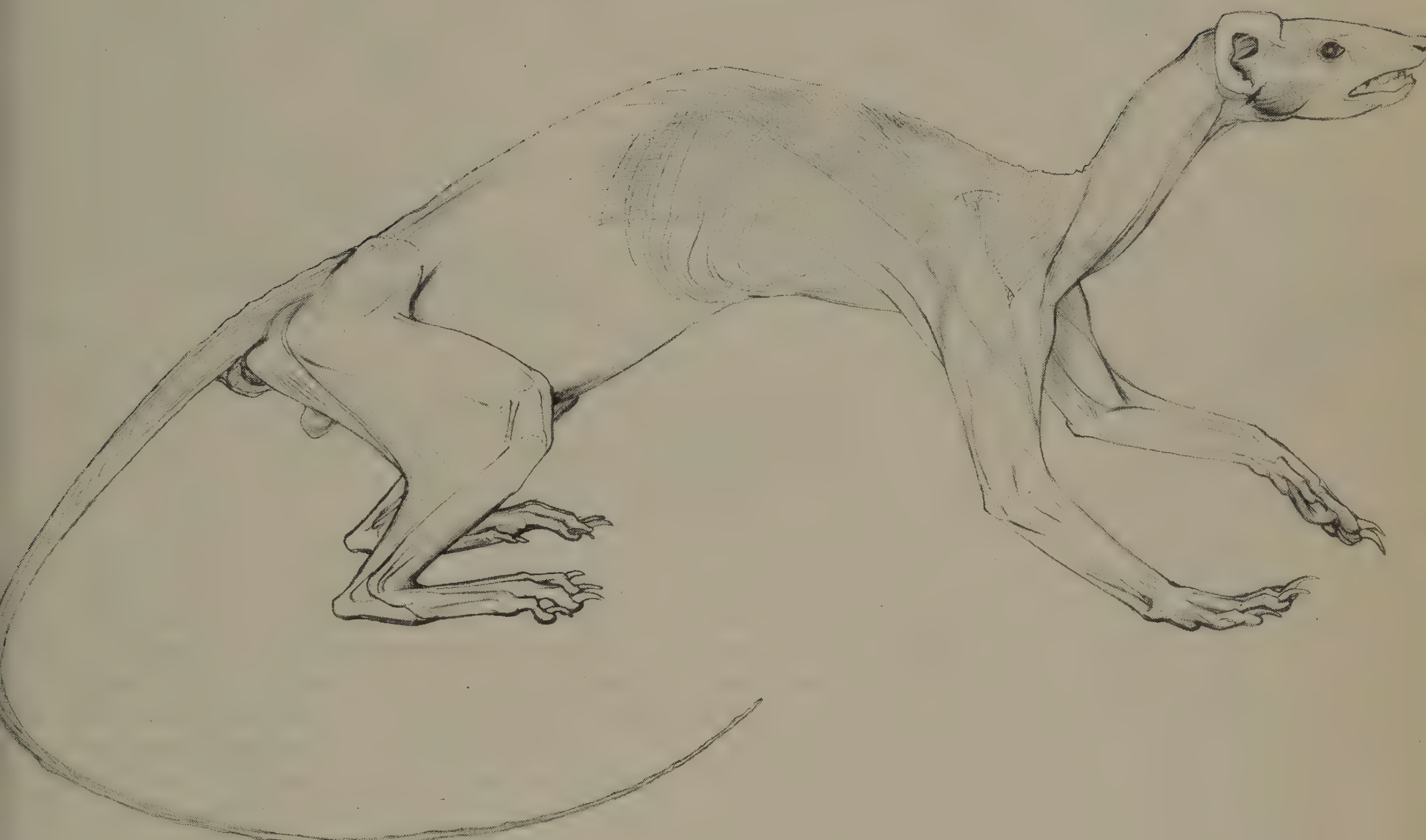
A captive I kept appeared to fascinate pied crows which would alight near its cage and, on several occasions, tried to peck at the black tip of its tail. Even monkeys have been seen to chase a mongoose that ran around in circles.

It seems reasonable, therefore, to suggest a fourth function, that of luring prey to the three anal chasing functions mentioned earlier. One should not, of course, have the impression that this is a routine way of catching prey since the animal's diet includes rodents and other small mammals, frogs, reptiles, crabs, eggs and even fish. Insects are often an important item in their very mixed diet and they have been seen digging in the dung of herbivores for beetles as well as picking up termites. Nevertheless, luring may be a major technique for capturing birds. Without regard to the prey species, ichneumons hardly ever chase their prey; they encounter it, instead, in the course of almost continuous exploratory walking. Because of their dense habitat their prey is usually come upon at close quarters and, if a single lightning strike with the jaws is unsuccessful, the walking and examining continues without interruption. Unlike its smaller relative, *Herpestes sanguineus*, this species is not a climber and, but for a few ground-nesting species, birds would normally be beyond its reach. Thus the slight modification of juvenile following behaviour elicits a very powerful mobbing or "curiosity" response in birds which brings them within the range of ichneumon's exceptionally speedy strike. Such behaviour is therefore essentially secondary to the fast strike, which must have developed as a result of the animal's dense habitat and was perhaps influenced by special requirements for killing snakes, which was described by Stevenson-Hamilton (1922):

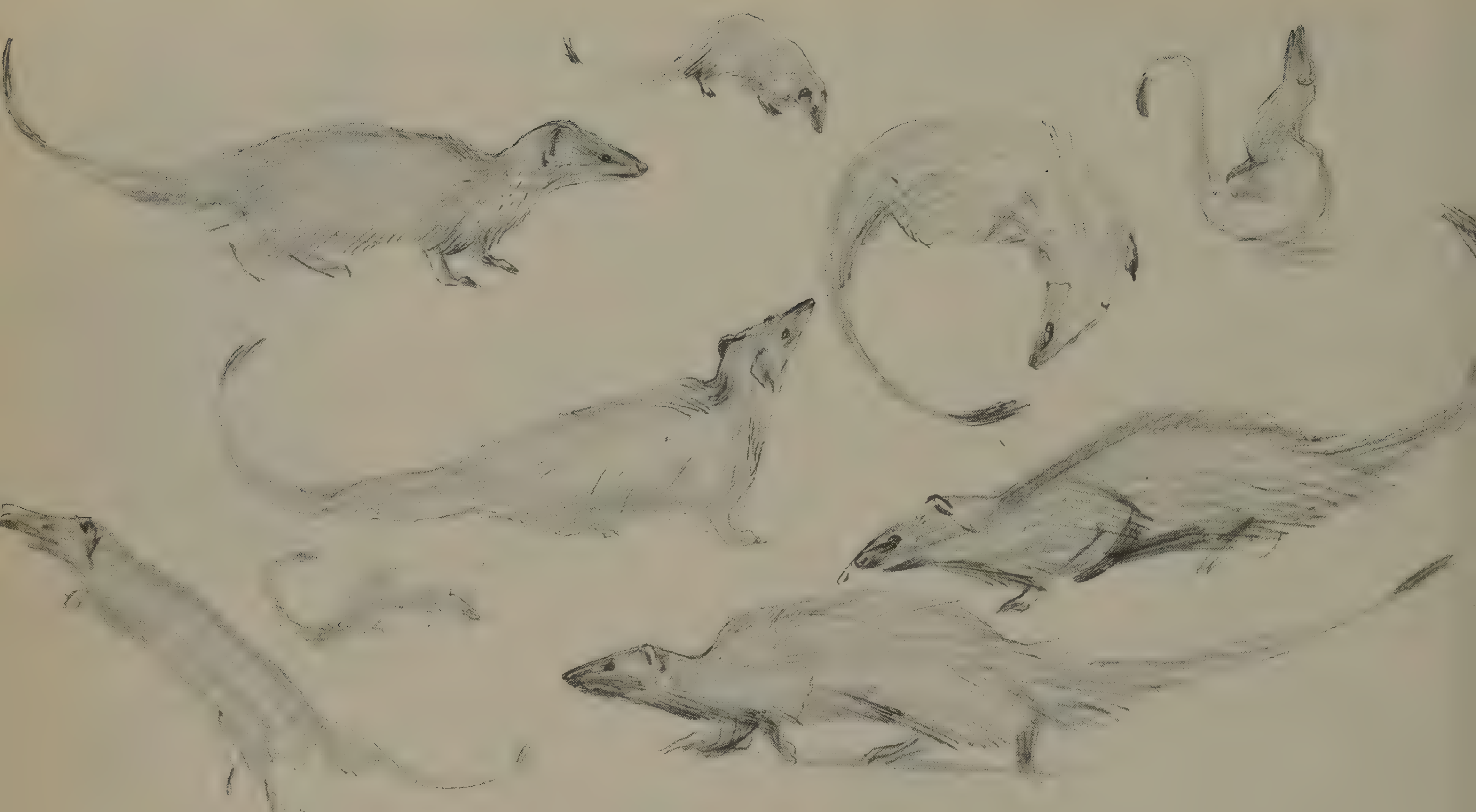
> "Their method is to run and bite the reptile from behind, jumping back swiftly to avoid its fangs and repeating the operation until they have killed it."

Tail-chasing behaviour often seems to be precipitated by an element of stress. Since ichneumons are only likely to be observed when in the open it could be that an animal adapted to dense cover is stressed when emerging into the open and, as birds are more likely to see the performance in an open situation, there could be a neat convergence here with the incidence of the behaviour.

The adhesive function of tail following has had brief mention but its role probably extends beyond the juvenile stage. While I have never seen more than two adults together, out of some scores of sightings in East Africa, there are numerous observations of larger groups (Rahm and Christiaensen, 1963; Roberts, 1951; Shortridge, 1934; Booth, 1960). De La Fuente (1972) reports Dr Valverde's findings that collective hunting is not uncommon in Spain.



Surveys in the Coto Donana show that about half the ichneumon population hunt on their own, the remainder being seen in pairs or in groups from three to seven individuals. When they hunt in bands, the mongooses forage intensively, continuously uttering little contact cries (behaviour that is reminiscent of *Mungos*). Animals are commonly seen in columns, each following immediately behind the animal in front. De La Fuente has also suggested that organized bands frequently roam a territory. The social proclivities of ichneumon in Spain might be encouraged by their being the only mongoose species. In East Africa, their niche could be circumscribed by the activities of *Mungos* and other sympatric species.



Territories or home ranges have not been investigated in East Africa. Dung deposits seem to be used with less frequency than by some other viverrids, although ichneumon are reported to revisit them from time to time.

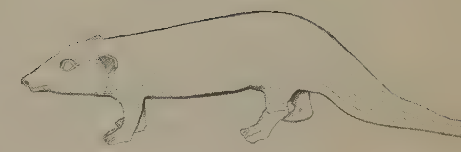
When captives play at fighting, they sometimes face off with arched backs and lashing tails and, when quarrelling over food, captives make explosive spitting sounds and may fall on their backs biting and clawing. A cackling sound signifies alarm. Rensch and Dücker (1959) have described their play in some detail; prey catching games involve the same patterns as real attack, with stalking, circling an object, rising on the hindlegs, waving of the head and pushing or seizing objects symbolizing prey. In the light of their habit of blind scent-following it is perhaps significant that captives also play a version of "blind man's buff" with their heads in a paper bag. Dücker (1965) has recorded the related Indian *Herpestes* retrieving a ball and returning it to the thrower.

This species is normally diurnal and in Coto Donana they are most active between 10 a.m. and 2 p.m., having emerged at dawn. I have seen them about at all hours of the day but never at night. They sleep with the head tucked under the belly.

Termitaries, culverts and a variety of natural crevices provide them with sleeping places and bolt holes and it has always surprised me to see a termitary or hole close by whenever they are pursued. Perhaps termitaries are characteristic of their choicest habitats; they are certainly slow at running and need a refuge from men and dogs. It is possible that venomous snakes bite them occasionally but the speed of their movements is likely to limit the

amount of poison that can be injected. Tests on *Herpestes pulverentulus* showed a tolerance of six times the mortal dose of poison for a rabbit but death ensued at eight times that amount (Calmette, 1907).

A transplanted member of this genus was discovered to be a discrete reservoir for rabies by Tierkel *et al.* (1952), when they found rabies in Puerto-Rican *Herpestes*, although the island had been thought to be free of the disease for nearly twenty years.



Ichneumon. Ancient Egyptian Bronze

In Kenya, Heisch *et al.* (1962) found antibodies for two types of rickettsia and Wier and Horsefall (1940) recovered a pneumonic virus affecting humans from a mongoose.

Human contact with members of this genus is very ancient in India. Skulls of *Herpestes* have also been found in Babylonian house excavations dated 600 B.C. In Ancient Egypt, ichneumon was associated with the gods Atun, Re and Horus (see drawing) and it was linked with the anti-snake-bite goddess Mafdet. Recognition of the diurnal habits of ichneumon was implied in the belief that it metamorphosed into a shrew during the night, a myth that apparently still persisted in Egypt in the nineteenth century.

Ichneumons tame readily and are popular pets and zoo animals. Dücker (1960) has described the mating behaviour of captive ichneumons in some detail. Oestrus is indicated by an extensive redness round the swollen vulva. After initial chasing, the female allows herself to be pressed down by the male and eventually signifies acceptance by raising the rump and turning the tail aside. A mutual mating call, rendered as "hai, hai" turns into a loud cackle resembling an alarm call. During copulation the male opens his mouth wide besides the female's nape but is inhibited from biting. Gestation is eleven weeks and in southern Spain there is a single birth season in July—August.

Verheyen (1951) asserted that there are two birth seasons a year in Upemba and repeated local reports that the young abandon the nest after a few days. In southern Uganda, newly born ichneumons have been recorded in September and February.

This species has lived nearly thirteen years in captivity.

Snouted Ichneumon (Herpestes (Xenogale) naso microdon)

Known from the Central Forest Refuge, this rare mongoose might occur in Bwamba or North Kigezi.

Herpestes sanguineus ("*proteus*" morph)

Slender Mongoose (Herpestes (Galerella) sanguineus)

Family Viverridae
Order Carnivora
Local names
Tuihu, Morunguru, Tungeni (Kikuyu), Ocuuli (Lwo), Echuli (Ateso), Lotuba (Karamojong), Kasisi (Lukonjo), Lukwiro (Kihehe), Ishinilye (Kinyiha), Tookabifa (Kiliangulu), Akategaruhende (Runyoro). *Note :* Local names for this animal are frequently interchangeable with those of a squirrel)

Measurements
head and body
26·8—33·8 cm
hindfoot
5·5—6·4 cm
tail
24—29 cm
weight
600 (425—683) g males
500 (350—515) g females
(Sizes vary regionally and males are heavier by about 100 g.)

Slender Mongoose (Herpestes (Galerella) sanguineus)

Nomenclature

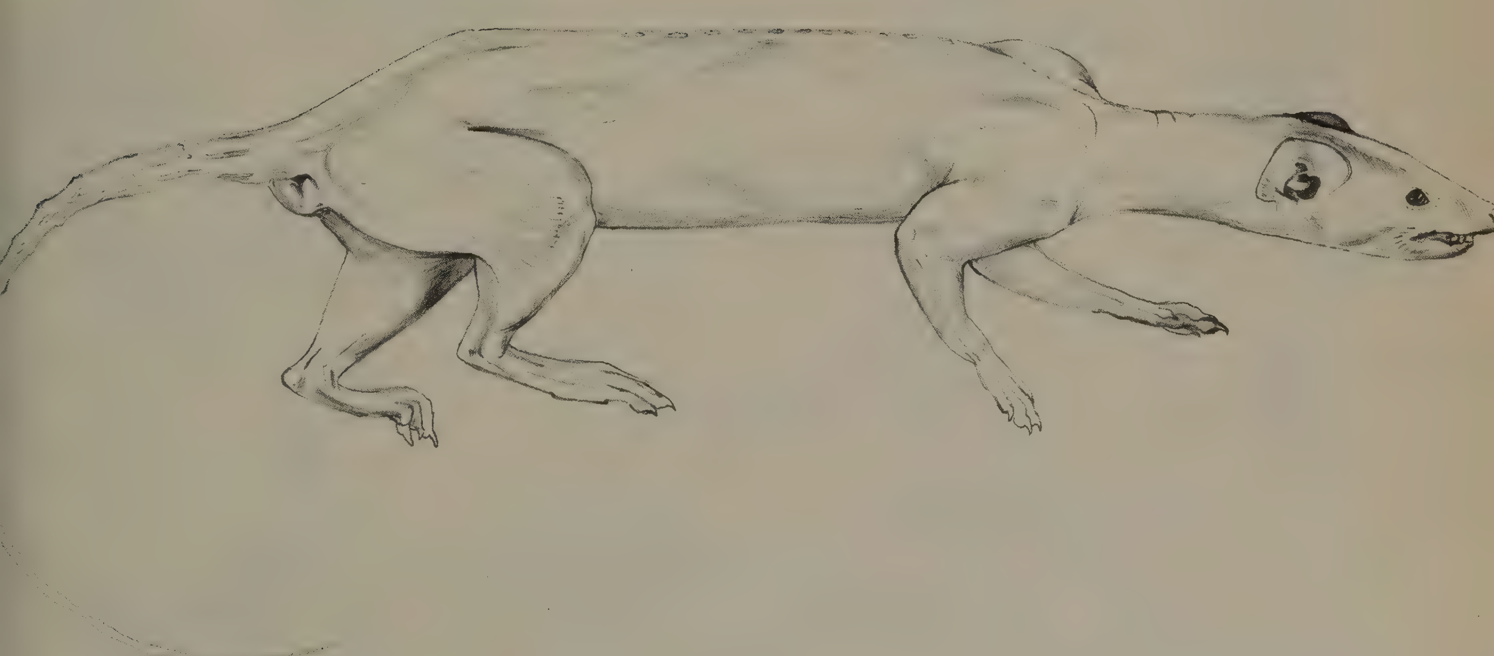
Sanguineus form

Grizzled short-haired. Pan-African distribution. Polymorphic in colour and over 40 races described. Names originating from East African animals are *conradei*, *dentifer*, *emini*, *galbus*, *ibeae*, *orestes*, *parvipes*, *proteus*, *rendilis*, *rufescens*, *ugandae*.

ratlamuchi or *ochracea* form

Plain shaggy hair, pale yellowish or reddish. Drier habitats in East and North-east Africa and perhaps in southern Africa. Includes *fulvidior*, *granti* and *perfulvida*.

Animals with a mixture of these characteristics are found in eastern Tanzania, i.e. *flaviventris*, *lademanni*, *mossambicus*.



These long-bodied, short-legged mongooses occupy a catholic range of habitats from scrub and thicket in the more arid zones through various wooded environments to high forest and papyrus swamps.

In such a ubiquitous species polymorphism may be an advantageous adaptation. Various shades of khaki (produced by pepper and salt grizzling) are the most commonly seen colours in East Africa but near black or very dark brown morphs predominate under humid conditions, notably in forest and montane habitats, and very light ones in drier more open country. Both extremes of colouring have been recorded in some localities together with intermediate forms and most populations produce colour morphs that differ radically from the one that is locally dominant. I have observed a wild yellow female (of *ugandae* or *galbus* type) mated to a nearly black morph (of *proteus* type). Their offspring was mahogany colour with a darker face.

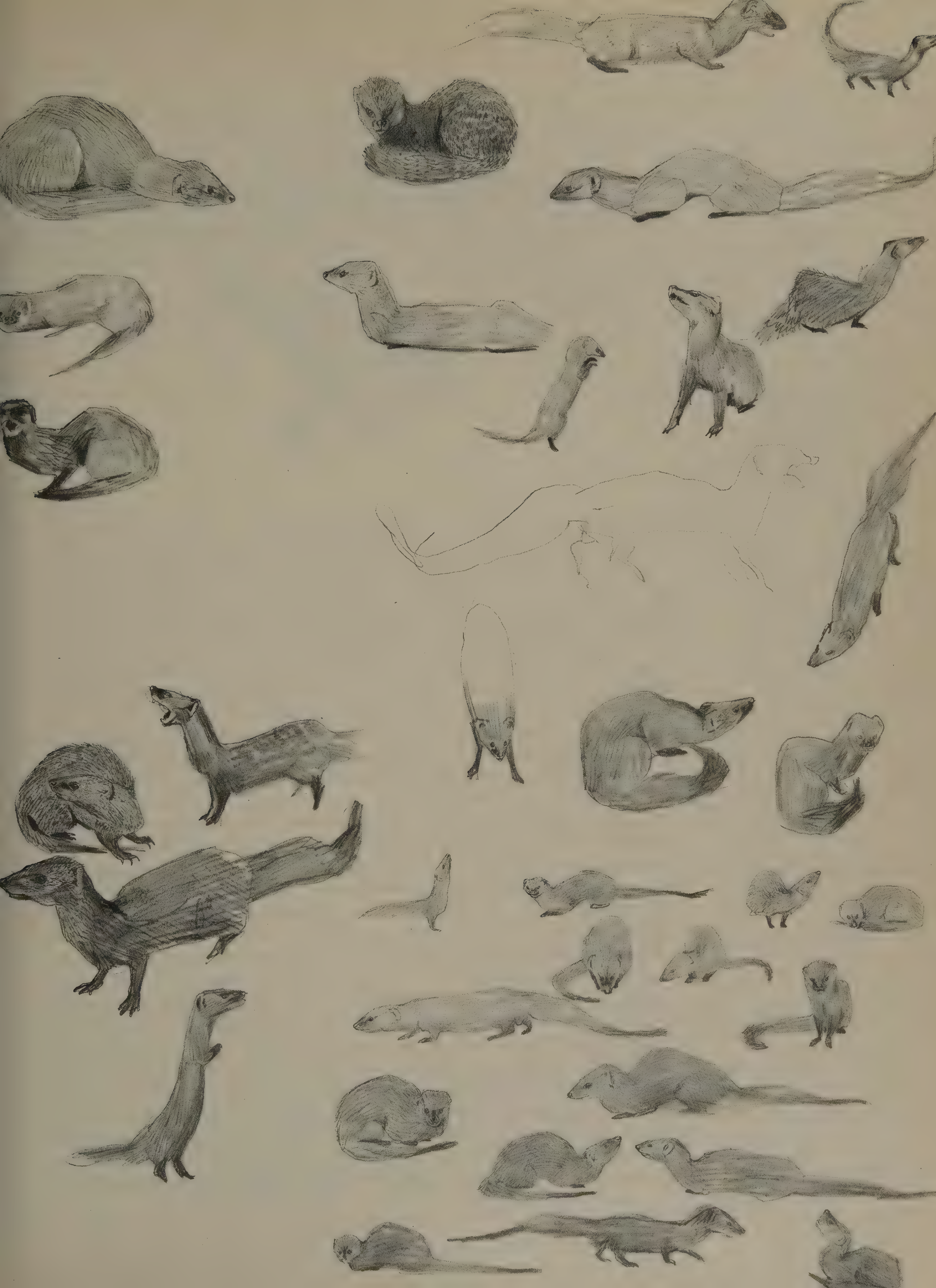
It is possible that *ochracea* originated through the isolation of one morph of an ancestral population in a dry habitat. However, there are now differences in the proportions of skulls, particularly in the auditory region, which suggest incipient or actual speciation. The distinctness of the two forms, however, is obscured by secondary mixing in eastern Tanzania, where apparently pure examples of *sanguineus* and *ochracea* coexist with types of mixed character.

This species must be numbered as one of the most successful and adaptable of the African carnivores. It covers a wide range of altitudes and probably occurs up to about 2,500 metres in montane forest. Although not as agile as a squirrel, this species runs up and down trees with great rapidity and I have seen it climb a succession of trees, apparently just to explore them briefly and then come down. Squirrels have in fact been recorded in their diet (Ansell, 1965), although terrestrial rodents probably make up the bulk of their food. I have found murid and insect remains in their dung and Verschuren (1958) found that eight out of nine stomachs in Garamba Park were filled with rats and mice; the other contained bird remains. Shortridge (1934) described them hiding amongst the branches of trees and springing out at small birds. They are frequently mobbed and this may allow them to kill unwary birds coming too close.

Other foods are chameleons, nestlings and eggs and, in South-west Africa, where they have been reported digging up groundnuts and coming to maize-baited traps (Shortridge, 1934), fruit and berries. Such foods are not common, however, and captives usually refuse fruit of any sort unless they are very hungry. Snakes and lizards are common foods and one has been seen trying to kill a large black cobra for about an hour, but without success. Toads and frogs have been recorded as well as various insects, including grasshoppers, cockchafers, termites and fly pupae excavated from the precincts of animal carcasses.

Cansdale (1946) writing in West Africa and Watson (1950) in Karamoja, both repeated assertions by local informants that this species displays its everted anal gland, which serves as a bait for birds but there are, so far as I am aware, no properly authenticated eye-witness accounts of such behaviour.

Their normal foraging gait could be described as built-in stalking. They glide along with the head down and their legs crouched; at intervals they halt and the head comes up with a smooth action, almost like a periscope in short grass, or they may rear right up on their hindlegs in taller vegetation.



Their movement is inconspicuous and I have seen them deliberately stalk ground-feeding pigeons after sighting them first in this way.

Birds and mammals are killed with well-directed bites at the neck and, starting with the head and brain, they tend to eat their way through everything, seldom leaving anything but a few primaries or tail feathers.

Although Shortridge (1934) described the South-west African desert form *swalius* as being active exclusively at night, I have no East African records of nocturnal activity and a wild family that took up residence in my garden in Uganda always emerged in the morning and retired while it was still daylight. This family established themselves in a tunnel drain while the house and garden were empty and the latter neglected. They apparently moved into the drain when the rains ended and slept there at nights, throughout the dry weather from June to September. I estimated the young one to have been born in April, so that the birth must have occurred in the rains in a separate den. As mongooses had previously been seen with some frequency near a large termitary about 150 metres away, it is possible it was born there. This site was in a heavily overgrown boundary hedge next to a main road and subject to much noise and disturbance. Although the female appeared to be the dominant animal and the male always kept a little distance from the mother and her young, the three lived amicably and occasionally even hunted together in a line, the male or female taking the lead but the young one always close behind the female. By October, after the rains had set in, the young one had reached adult size; the trio left the drain but continued to spend some time in the garden. At this time there were some very violent and noisy fights within the family, but as these mostly took place in the thick cover it was not certain which animals were involved. However, on one occasion it was almost certainly between the adults and immediately afterwards I saw the female suddenly start to groom the young one. As the male approached, she gave every sign of nervousness and I had the impression that the male was threatening the young and the female was threatening the male. Thereafter only the male and female were seen but with less frequency and generally on their own. The female was unfortunately run over a month later (see drawing) but a male mongoose of identical dark colouring continued to be seen at intervals over the next five years, always alone. This was probably the same male and it was seen occasionally within a radius of some

Herpestes sanguineus
("*ugandae*" morph)

500 metres of the house. That the ranges of males can overlap has been confirmed in sightings of two males foraging within sight of one another. Otherwise adults appear to be intolerant of other adults of the same sex.

Taylor (1970) estimated a range of about one square kilometre on the basis of trapping records on a farm in central Kenya, but Ansell (1970) had the impression that the range of his free-ranging juvenile was always within earshot of his house. A similarly diminutive range applied to my family but only for the period of the young one's growth. When it was about sixteen months old Ansell's female became aggressive towards him—he seems to have acted as a surrogate parent. This behaviour is very interesting in the context of my observations on the disintegration of a family and the dominant role of the female, and the species would seem to be a promising candidate for a behaviour study.

Apart from screeching when fighting, the only sound I heard was a somewhat bird-like whistle, which was rather rare and presumably functioned as a contact call. They are reported to make a scolding cry of alarm. Rather like *Mungos*, this species will occasionally drag its belly over grass but I seldom saw them anal mark nor were there signs of regular dung deposits.

Slender mongooses are sometimes kept as pets and attach themselves very closely to individual keepers. One such mongoose slept on its owner's pillow and could not be induced to sleep elsewhere. It also rushed to share its keeper's drink, jumping on to a shoulder and pushing its face and paws into the glass. Its favourite game was to rush up suitable trees or roofs and slide down their inclined surfaces (Mrs Fulton, personal communication). This pet occasionally indulged in fits of marking activity, walking backwards as it produced a strong smell from its anal glands. At this time the animal also excreted and its body went rigid. It is interesting that, in spite of its normally following a diurnal activity pattern, the marking ceremony only occurred at night.

These mongooses interact with many of the animals they come across.

They have been seen to chase playfully small antelopes and hyraxes on the ground and even a colobus in a tree. Ground squirrels have been observed to initiate chases by approaching the mongooses very closely before turning tail and rushing off (Root, personal communication).

The development of a young slender mongoose from the age of a month to adult size at six months has been described by Ansell (1970). He noted that the eyes of this young female turned from olive green to reddish amber and it is possible that this sign of maturity may be one of the signals for parental intolerance. Another animal that was completely intractable when first trapped as a subadult in a Uganda papyrus swamp changed its behaviour instantly after its trapper seized it by the scruff of the neck. The firm handling appeared to induce intense submission, after which it became quite tame (Prentice, personal communication). Verschuren (1951) caged one with a *Mungos mungo*, which led to much fighting and an intense fear of the slender mongoose on the part of the striped one.

On the basis of his trapping in central Kenya, Taylor (1969) thought there was a correlation between breeding and the biannual rains but could not show that individual females necessarily bred twice a year. The Uganda female that was run over some eight months after giving birth showed no sign of being pregnant again.

Asterly Maberly (1963) mentions this species as a victim of rabies and Heisch *et al.* (1962) found antibodies for rickettsia. Loveridge (1923) found nematodes and flea parasites.

I have encountered this species far out in the middle of papyrus swamps in Uganda, where they will climb papyrus stems. The animal represented in

a sixth dynasty Egyptian bas-relief on the Mastaba de Mererouka at Saqquarah (pictured below) conceivably represents this species being mobbed by a pied kingfisher. This relief shows a restraining hand on its tail, implying that the animal was either hunted or actually used for hunting (see Keimer, 1942). Other reliefs at Thebes are pictured in Wilkinson (1878). Possibly the slender mongoose was well known between 2,800 and 2,150 B.C. on the lower Nile, an area where it no longer exists.

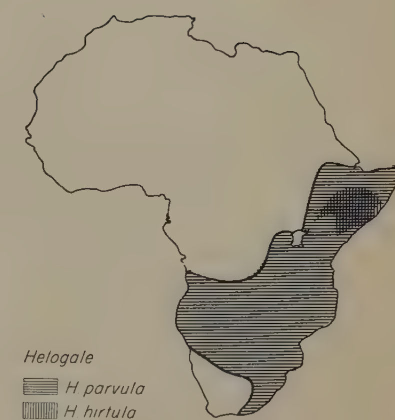
Dwarf Mongoose (Helogale)

Family Viverridae
Order Carnivora
Local names
Kitafe (Kiswahili), Kamsio (Kinyamwesi), Lonzi (Kiramba), Kijinola (Kisukuma), Miniyrsira, Nkhamenungu (Kinyaturu), Chunchulo (Kiliangulu), Lojute (Karamojong), Muloli, Sala (Kigogo), Ocunli (Lwo), Munyuru (Kitaita), Kingalla (Kisagara)

Measurements
head and body
18—26 cm
hindfoot
3·8—4·6 cm
tail
12—20 cm
weight
300 (230—680) g

Dwarf Mongoose (Helogale)

Dwarf mongooses are extremely variable in colouring and many of the numerous races that have been described are invalid. Coetzee (1967) has provisionally recognized two species and this course is followed here.



Species (Provisional)

Helogale parvula	Short glossy fur. Length of upper premolar 4—4·4 mm.
Helogale hirtula	Arid habitats, more shaggy fur. Length of upper premolar 4—exceeds 4·5 mm.

With small features and a smooth finely grizzled coat, the dwarf mongoose is easily distinguished by its small size and, in the field, by its normally social habits.

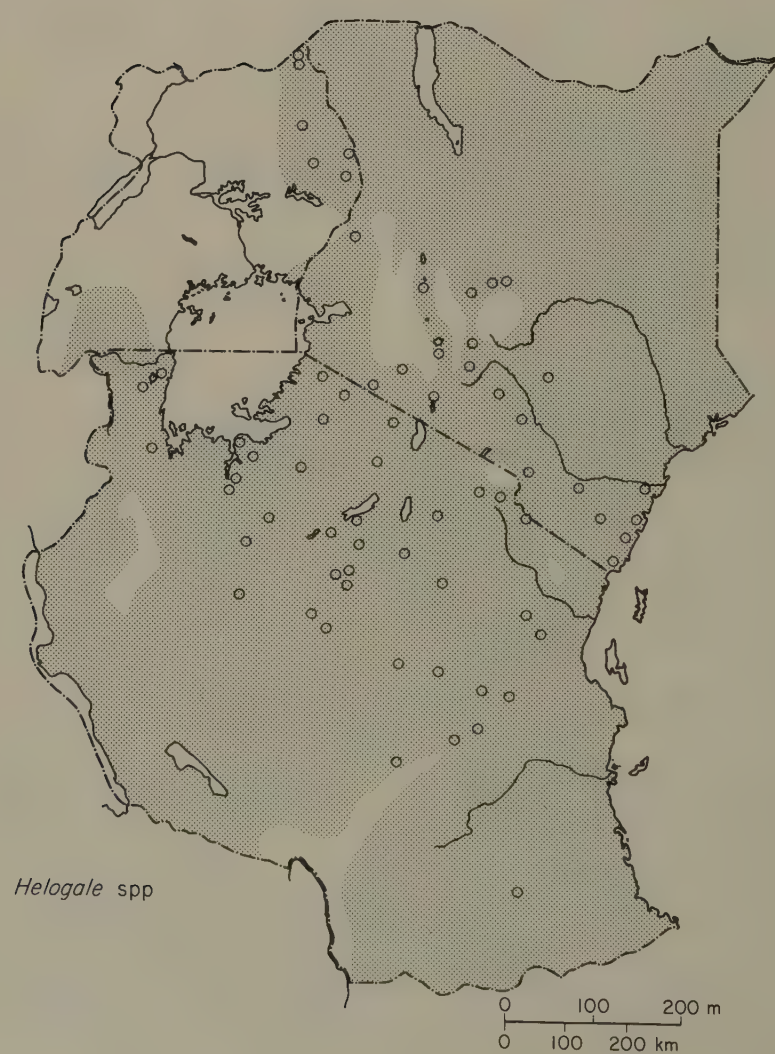
The dominant species, *H. parvula*, is distributed through a very wide range of bush and woodland habitats in southern and eastern Africa. *H. hirtula*, instead, is an arid-adapted form from the Horn of Africa but the distribution of the two species overlaps extensively. These little mongooses appear to be very sensitive to cold and they are not found at altitudes above about 2,000 metres. Captives taken to colder climates like to bask in front of fires and will go into a coma if exposed to winter temperatures, becoming quite stiff, a condition from which they have been known to revive but which may equally well lead to death.

Helogale are particularly common in areas with plenty of termitaries and it is possible that an abundance of shelters encourages survival in spite of their readiness to dig holes by themselves. Termites also occur in their diet but I do not know how commonly these include the mound-building species. They mainly eat insects and their larvae and a wide range of invertebrates, small vertebrates and fallen fruits; scorpions, myriapods, spiders, worms, slugs, snails, frogs, rodents, reptiles, birds and their eggs have all been recorded.

Most of the cryptic fauna and larvae are excavated from decayed wood, earth or crevices by rapid and determined scratching after sniffing and listening. Immobile prey is eaten alive, while anything attempting to escape is killed with well-directed bites at the head. All but the hardest parts of the prey are eaten and small mammals and birds are often partially skinned or plucked. Hard-shelled eggs are thrown backwards against a stone or stump, but the motive force is sometimes exerted by the back legs instead of the front ones, the animal jumping up as it does so and landing on its forepaws. Flying termites are leapt after with wild flailing of the tail and clutching with the paws. Like *Mungos*, some foods are occasionally marked with the cheek and anal glands. Several mongooses will sometimes join in an attack on larger

prey such as a snake or a rat and I was told by a farmer in Kenya, Mrs Betty Fulton, that rats were virtually suppressed while a large pack lived around her farm but, once the number of mongooses fell to four or five the rat population reasserted itself.

I am indebted to Mrs Fulton for much of the information that follows, as she was able to watch this pack at close quarters over a period of seven years. Over the years this pack was in residence, the elimination of rat damage and the saving in spoiled produce was worth hundreds of pounds and this could be attributed primarily to the mongooses ferreting out the rats' nests wherever they were, as well as to their ability to kill adult rodents. The other side of the coin was the necessity to make the quarters of egg-laying birds mongoose-proof and mongooses were often seen hooking a fresh egg out from beneath a duck while the bird's pecks were fended off with the unengaged paw.



An interesting association with a pedigree bull started as the result of a solitary male mongoose stalking and pouncing on the grasshoppers that were disturbed while the bull grazed. The shelter afforded by the bull encouraged the mongoose to venture out with it into the open and eventually the mongoose took to resting on the bull's head and shoulders whenever it lay down. The bull seemed to combine the amenities of a living companion, a food provider, a mobile vantage point and a shield against enemies. However, the increased exposure finally led to the mongoose's being taken by a hawk.

Normally the alertness of a single mongoose is augmented by that of the other members of the pack, spread out over 50 to 60 metres in the skirmishing line that they commonly adopt while foraging. The entire pack will race for cover at a warning cry from the exceptionally alert juveniles; this is a very shrill explosive double note.

While foraging, the entire group keeps in touch with a tinkling vibrating chirrup. Possessive over any bit of food they may have, individuals threaten one another with a growl or scolding churr and a sharper more explosive churr is directed at dogs, snakes, monkeys or other animals that might disturb or endanger them. Bluff attacks with rushing feints and retreats are punctuated by these cries and are started mainly by adult males. Excitement at a plentiful cache of foods or while marking is sometimes accompanied by an outburst of shrill twittering. The young have a very characteristic distress call with a prolonged cheep at the end, which can be rendered as "ti-ti-teeee". The alarm call elicited by hawks and other large predators is a shrill shriek, to which many of the mongooses respond. This call is most frequently initiated by the juveniles.

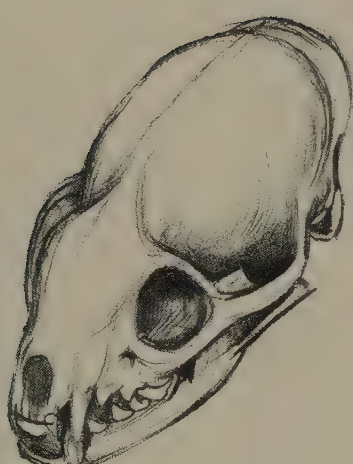
Like the other mongooses they engage in much marking activity, frequently standing on the forelegs to do so and applying secretions to one another and to all sorts of objects in the surroundings. Zannier (1965) described the persistent head-rubbing of this species and drew attention to inconspicuous skin secretions from the cheek region. The anal gland, instead, is a prominent and specialized structure. Animals frequently groom their own anal area, and lick the gland. This sometimes follows a chase after its own tail by a young animal and a line of mongooses each with their nose adhering to the other's tail will occasionally form. A curled sleeping position is sometimes assumed after some sniffing or licking of the gland. However, this is not a preferred area in social grooming, which is directed instead mainly to the neck and other parts inaccessible to the individual on its own. In a tangle of resting animals it can often be seen that many of them have settled down with their heads on the napes of others. Animals usually groom the underparts and limbs themselves by nibbling and licking, and they even insert their claws into their mouths in what Zannier (1965) described as tooth cleaning. A mongoose soliciting grooming from a fellow often stretches its legs upon the ground and drags itself forward on its belly.

Their normal gait is a quick trot, with the head and tail more or less in line with the body. When alert they may stand on their hindlegs and bob their head up and down but they do not stand as frequently as *Mungos*. Although they often climb short distances up trees, particularly sloping trunks, they are not skilled at it.

All members of the pack deposit their faeces in the same spot but this is

generally not in an exposed position and they prefer corners or crevices not far from the sleeping den. One spot is used for several weeks and then changed; urine is also deposited in a shared latrine but this is generally separate from the dung deposit. They defaecate in the early morning after emerging from the hole.

The timing of their emergence depends to some extent on temperature and the normal dawn rise may be delayed on cold mornings. They hunt intensively in the early morning and again between 4.30 and dusk. Hunting is often terminated quite abruptly in the morning with an individual's stopping to groom itself. Others follow suit and some parties of mutual groomers settle down to nibble one another's necks. They may retire to the burrow or lie about outside for their afternoon sleep during the heat of the day and the subadults which remain most alert during this period often start competitive wrestling games in the late afternoon, rising on their hind-legs and turning to throw one another off balance.



The social organization of most mongoose genera centres on the mated pair and their offspring. This fundamental pattern is retained by *Helogale* but it has involved the suppression of breeding in other members of the extended family and a very interesting specialization of roles. The first published reference to this was by Rasa (1972, 1973a) studying a captive group in Germany, but this phenomenon had been known for some time to several East African residents with intimate knowledge of wild groups and who had bred wild families. Although I have heard of two instances where more than one female in a pack produced litters, this is not usual either in captivity or in the wild.

Two wild packs known to me numbered 40 individuals. In each case they were living a semi-protected existence close to human activity (on a farm and by a National Park lodge). This may have substantially reduced losses by predators; a common average cited by observers is twelve animals. That the home burrow needs a protected site is implied by Roberts (1951) trapping

them besides a bees' nest, a situation which apparently afforded protection also for a large number of hyraxes, *Heterohyrax*, rock rats, *Petromus*, and shrews, *Crocidura cyanea*.

Mrs Fulton was able to watch the entire development of an extended family over a period of seven years (1962—69). The original pair started breeding at the estimated age of three years and they remained the recognizable seniors of the extended family over the whole period. The breeding female is in every respect the dominant individual. Together with young less than three months old, she has absolute and unchallenged priority over any food item, a peculiar status in an animal where every individual hunts for itself and normally guards its own forage jealously; but, as Rasa (1972) points out, this system ensures that food goes first to those that need it most. Although the breeding female, like any other adult, will allow babies to take food out of her mouth, she will not allow any other class near her while she is foraging and will appropriate food from any mongoose she sees eating.

She also initiates all movements, whether setting off in the morning or returning home at night, with distinct trilling calls which are peculiar to her alone. In fact, she has a longer vocabulary than any other class of mongoose. In response to one call, small babies are picked up by their "nannies" and to another, the whole group moves off in a "V" formation behind her; with more urgent chitter from her—most commonly made in the late evening—she leads the pack in a rush to the den, where they spend the night sleeping in a pile of bodies.

The matriarch is never far away from the family, which shows signs of nervousness without her, but she goes through a semi-solitary phase for about three weeks to a fortnight after the birth of each litter. After this brief spell of semi-independence she again becomes the full-time matriarch of the tightly-knit group, whose formation Shortridge (1934) likened to a pack of beagles. Her independence is made possible by the fact that, apart from producing milk, she has no responsibility towards the young at all.

The young are cared for by non-breeding adults of both sexes, amongst which there is intense competition to groom and carry the young. Among the most avid of these "nannies" are the generation between six and nine months old, which bring the young to the mother for suckling—the stimulus for this attendance being the mother's lying down and stretching out on her side. There is generally a single dominant male, which is subordinate to the matriarch only, and his role includes defence. Mrs Fulton even saw the dominant male hold the mother down after bringing her an infant to suckle. Attempting to keep a female caught alone with her litter of four, Loveridge (1923) noted her refusal to suckle in spite of maintaining her own appetite and health, her neglect being due, no doubt, to the lack of ministrations from the "nannies".

A further stratification of function is apparent in the extended family. Litters are spaced between nine and twenty-six weeks apart and the privileged status of the former infants is lost instantly on the arrival of the new ones; tenderly cossetted by all one day they are completely ignored the next. After about three days of cheeping in distress, this generation begins to assume a special role in the family, which may well be the product of this trauma. They are particularly nervous and alert so that any passing hawk or dog is almost

invariably detected by the members of this age-group before the others. In fact, it is possible that other classes are less alert and that in a fully structured extended family, they actually rely on these juveniles to act as guards. Possibly repelled by the adults indifference or by inconspicuous aggression, the juveniles' nervous disposition may also cause them to occupy the periphery of the pack; thus around a nùcleus of babies there are older "nannies" and then juvenile guards. Meanwhile the matriarch may be foraging outside the group or in its midst depending on the stage of her own cycle.

Helogale pack dispersal

Studying a captive laboratory colony, Rasa (1972) recognized that activities such as guarding or baby-sitting influenced social bonds between individuals. In spite of the rarity of overt aggression, Rasa found a single linear hierarchy in this colony, which was ranked by age groups, in each of which females dominated males. She revealed rank by repeated scoring of the order of precedence for each mongoose at a source of food and at an object being marked with the glands. The matriarch and her consort were termed the alpha animals and Rasa (1973a) spelled out the rest of hierarchy as juveniles (under one year) followed by subadults (in her colony this age-class was one to three years old) and then adults. She described each generation of mongooses dropping lower with the arrival of a new litter and each individual finding its position by reference to its litter mates, but the generation time and age of maturation of her colony in Germany was twice that observed in Kenya. Because there are functional differences in the roles played by particular generations, the actual age of which is variable, it is the sequence rather than age of a litter that is the more significant for social structure in *Helogale*.

Rasa (1973b) thought that the alpha male prevented breeding in her mongoose colony by actively intervening in any form of heterosexual

behaviour among siblings and she described this male threatening such pairs. She also pointed out that both mounting and grooming were more frequent among animals of the same rather than the opposite sex. In those rare packs where more than one female produces a litter it would be interesting to know whether both animals are inseminated by the dominant male; Rasa's captive alpha male showed no interest in females other than the matriarch and all other group members were driven off by him when she was in oestrus. It is possible that a combination of female dominance and harassment by the alpha male suppresses heterosexual behaviour in the other males. The fact that other females can occasionally conceive demonstrates that the behaviour and biochemistry inhibiting breeding can break down but the mechanism remains uninvestigated.

Mrs Fulton thought the oestrous cycles of non-breeding females were rather irregular in contrast to the matriarch's. In this wild pack, oestrus was recognized subjectively by a definite change in a female's behaviour and by an increase in marking behaviour and by her interest in the males. Instead of responding, the males, most particularly the dominant male, drove these apparently receptive animals right out of the group. Males would occasionally gang up against a female and attack her quite severely and one particularly tame female watched by Mrs Fulton was inexplicably attacked in this way.

Although it has never been recorded, it is theoretically possible that this is one of the points at which a female could hive off and start a new family with a young male. However, the observed build-up of numbers around a

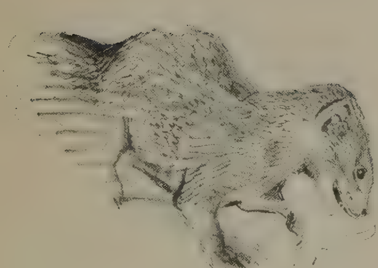
single pair suggests that normally the cohesive forces within an extended family are sufficiently powerful to stop this from happening. While a subsidiary female is in oestrus, she is kept out of the pack until her oestrus is over, after which she rejoins the family as a full member.

The most likely mechanism for the formation of new families is the death of the matriarch. In the case of the family watched by Mrs Fulton, this happened when she was heavily pregnant and very slow. The group numbered 24 at the time of her disappearance and the entire family wandered about searching and making want calls typical of juvenile behaviour. They then started disappearing, some presumably wandering further and further afield and in less than six weeks only three animals remained within the old range.

The rich resources of a large farm and its complex of buildings encouraged the small range of this family, which spent virtually all its time within an area of two hectares. After the dispersal of the family, the remaining three animals travelled over a distance of 1·6 km, spending several days on another farm before returning again for a while.

A pack in the Tsavo Park regularly spends the long dry season in the immediate vicinity of a lodge—also an area of about two hectares—but with the arrival of the rains and longer grass they move off and are not seen for about six weeks (Hindley, personal communication). At such times they are probably fairly mobile and Shortridge (1934) characterized dwarf mongooses as animals "of no fixed abode" but having favourite feeding grounds to which they tend to return. Termitaries and other dens are frequently modified by the mongooses' digging and they dig extra concealed exits and entrances.

There is no doubt that extended families are closed societies completely intolerant of strangers. Even members of the same family are killed instantly if they are removed long enough to be forgotten; they appear to be identified by scent. Rasa (in Ewer, 1973) has explored the glandular messages of captive *Helogale* and she evoked a threat display by presenting them with secretions of a conspecific smeared on a glass slide. She has also shown that a mongoose can tell the difference between the anal sac secretions of different individuals and that the secretion of an unfamiliar animal arouses interest, without signs of fear or aggression. It would, therefore, seem that in this species the anal sac secretion carries no specific threat but is quite simply the personal signature of the animal that made the mark. Cheek glands marking, on the other hand, is an olfactory threat but it is an anonymous one; it does not carry a personal signature. In fact, the signature is always added, for animals never mark with the cheek glands without also marking with the anal sac. Another interesting point discovered by Rasa is that while the anal sac mark lasts for something in the order of a fortnight, the olfactory threat is short-lived and the smell is no longer detectable by the animals after 48 hours. The adaptive significance of this is clear; the signature indicating the animal habitually frequenting the area is lasting, but the threat, which presumably relates to some specific incident is not (Ewer, 1973).



The cheeks are rubbed on a variety of natural objects as well as on the young, which are then slid between the legs to be marked with the anal gland. Apart from the normal bottom-dragging posture there is the handstand and curiously dog-like lifting of the leg to urine-mark. The entire mongoose

community is enmeshed with its environment in a continually renewed net of scent marks.

Zannier (1965) described marking and sexual behaviour in a captive pair in great detail. An increase in marking by both sexes heralded the onset of oestrus, which lasted three days. The female's vulva became somewhat red and swollen and there was much mutual sniffing and licking of the genital area. After a number of attempts, the male was eventually permitted to mount and copulation lasted about five minutes with the male biting and nibbling the female's neck. Zannier (1965) estimated the gestation period at 50—54 days and an average of four (two to six) young are born. There is a post-partum oestrus which may recur after a 21—24 day cycle. If she fails to become pregnant, another cycle follows. The interval between litters averages about ten weeks, allowing four generations a year, giving a potential annual recruitment of about sixteen. In Tsavo, the extended family already referred to doubled its numbers from 20 to 40 in three years (Hindley, personal communication) so that in spite of a somewhat protected site the survival of the young was well below 50%.

For about three days before parturition the female remains on her own in a nest she has made herself in some dry secluded crevice or hole in a termitary or, according to Stevenson Hamilton (1923), in long grass. Wild mothers do not allow any other adults near for this period.

Zannier (1965) had a *Helogale* which gave birth at the age of five months, yet two older female survivors of the matriarchy watched by Mrs Fulton failed to breed although they were accompanied by a male. Rasa (1973b) only saw a first oestrus in subsidiary females when the animals were over two years old.

The infants are relatively large and are well-haired but blind at birth. It is possible that just before and after the birth other members of the extended family feed the mother as they have been seen carrying food home to the burrow at about this time. Suckling periods are very short after the first day and there are intervals of three to four hours. The young purr while sucking. Any disturbance of the young may lead to a change of quarters and the members of the extended family will attack in concert any predator interfering with young infants. The eyes open at about thirteen days and this coincides with their first exposure to the open, where they spend short periods in the sun. Although a sun-bathing expedition is initiated by the mother, each young is usually carried, curled up and held by the scruff of the neck, by a six-month-old sibling and, although all classes and sexes hug and play with the young it is mainly the recently mature that fetch and carry. When two compete, they sometimes pull the unfortunate baby in opposite directions. Nonetheless, handling is gentle and casualties from such treatment are not known.

Weaning is accomplished very rapidly after the third week and adults bring food, which they push into the mouths of the young when they are three weeks old. Jacobsen (In Ewer, 1973) found that the male was particularly assiduous in attending to the young. Soon the young begin to join in foraging expeditions and the adults' tendency to withhold food starts reasserting itself; this becomes an incitement for the young to grab and soon they are actively stealing and then catching items for themselves.

With emergence from the burrow, play becomes a major activity of the young, in which adults often join. The termitary becomes a good site for what might be hierarchy-determining or "king of the castle" games, in which siblings compete to dislodge a fellow off a commanding position and there is much wrestling, mock fighting and pouncing. Playfulness, which begins at four weeks of age tends to come to an abrupt end with the arrival of the next litter. At about this time, marking and other adult behaviour is also acquired.

While many mongooses are probably taken by hawks, their continuous exploratory behaviour often gets them lost, and mummified casualties in odd places were sometimes found on Mrs Fulton's farm.

Dogs, cats and snakes are often baited by the whole family, with at least one of the horde of spitting and churring mongooses jumping back and forth with snapping jaws. In this way some dogs and other predators may be intimidated but the penalty for such audacious behaviour must be many casualties.

They are eaten in some areas, and also unfortunately persecuted as egg thieves, a proclivity that is more than made up for by their capacity for killing rats.

Captives have reached the age of ten years.

Savanna Mongoose (Dologale dybowskii)

Family	Viverridae
Order	Carnivora

Measurements
head and body
25—33 cm
hindleg
5·5 cm
tail
16—23 cm
weight
300—400 g (approx.)

Savanna Mongoose (Dologale dybowskii)

This small mongoose has a close resemblance with *Helogale* in size and appearance. It is dark brown and grizzled all over except that the head is somewhat darker and the limbs are almost black. The forefeet carry robust digging claws. It can be distinguished from *Helogale* by the absence of a groove in the upper lip.

This monospecific genus is known from rather few specimens collected in Uganda, eastern Zaire and southern Sudan. It has been found on the hot low-lying and thicketed shores of Lake Albert, in the savanna-forest mosaic of Mubende and in the montane forest grasslands of the Imatong Mountains. It therefore seems to be fairly adaptable as far as habitat goes. Its rarity may be due simply to shy habits and a paucity of naturalists in its habitat. I have seen a mongoose that was almost certainly this species in Singo, where it took refuge in a termitary. This one was on its own and no mention has been made by collectors of seeing them in packs. This is curious as the animal is somewhat intermediate in character between the social Helogale and the *Mungos-Crossarchus* groups, although very much nearer the former.

Dologale dybowskii

It is possible that this is a relic species living in an ambiguous overlap zone that lies between the true forests and the drier bushlands and savannas where *Helogale* is a dominant mongoose. *Mungos mungo* is an obvious competitor but the diversity of habitats and equable climate in Uganda and north-eastern Zaire may encourage an equal diversity of opportunities and reduction of competition.

Given its close relationship and the possibility that it may be less social than *Helogale* it would be of the greatest interest to know more about the social organization and general biology of this species.

At present nothing whatever is known. Dorst and Dandelot (1970) suggest that it may be at least partly diurnal and hide in hollow trees and termite mounds, which accords with the mongoose I saw at about 9 a.m.

Their diet is unlikely to differ greatly from that of *Helogale* and *Mungos* and their digging claws are particularly suggestive of similar habits to the latter.

Marsh Mongoose (Atilax paludinosus)

Family Viverridae
Order Carnivora
Local names
Nguchiro cha maji (Kiswahili), Eggunju (Luganda), Ogwang anyeri (Lwo), Kimajukare (Lubwizi), Amazukara (Kuamba), Chihura (Lukiga), Lunamatu (Kiragoli), Linsi (Lugisu), Mugoeet (Masai), Mkekwa (Kinyakyusa)

Measurements
head and body
46—62 cm
hindfoot
9·5—10·5 cm
tail
32—53 cm
weight
2·5—4·1 kg

Marsh Mongoose (Atilax paludinosus)

Atilax paludinosus.

This large dark-brown animal is one of the more highly specialized mongooses, yet like its relatives it retains a relatively generalized body plan. Its versatile habits enable it to cope with drastic seasonal changes and to exploit a wide range of swampy conditions.

The neck, body and tail are well covered with thick, shaggy fur but the extremities have naked palms and short sleek fur over the long-fingered hands and feet. This mongoose normally catches its food by wading into shallow, usually muddy water and feeling for its prey, so the change in fur texture above the wrists and ankles indicates adaptation to the role of a wader. The hands are extremely soft, without thick tissue and are probably very sensitive organs. The "thumb" is mildly opposable but it functions more as a passive prop, enhancing the animal's purchase on a slippery object rather than providing an independent grip. The premolar teeth are stout and well-adapted to crushing hard foods and the lower canines are particularly well developed.

The marsh mongoose is widely distributed over all the better-watered parts of Africa, even surviving in areas with quite a severe dry season. It ranges from sea level up to about 2,500 metres, with a preference for swampy vegetation bordering rivers and lakes but Booth (1959) recorded it in hills near Accra where there was little water and no aquatic fauna to feed on. Above all, marsh mongooses are an important member of the small community of animals specially adapted to *Papyrus* swamps and it is possible that their evolution may have centred on exploitation of this vegetation type. Papyrus swamp has been estimated to cover nearly 30% of the land area of Uganda, yet it is the habitat of a very restricted number of species. This is mainly due to the deoxygenated water so that the main aquatic inhabitants are the air-breathing lung fish, *Protopterus*, and catfish, *Clarias*, frogs, insect larvae and snails. I have found numerous mongoose droppings in papyrus swamps, mainly made up of the remnants of these types of food with some bird and rodent remains and traces of vegetable matter.

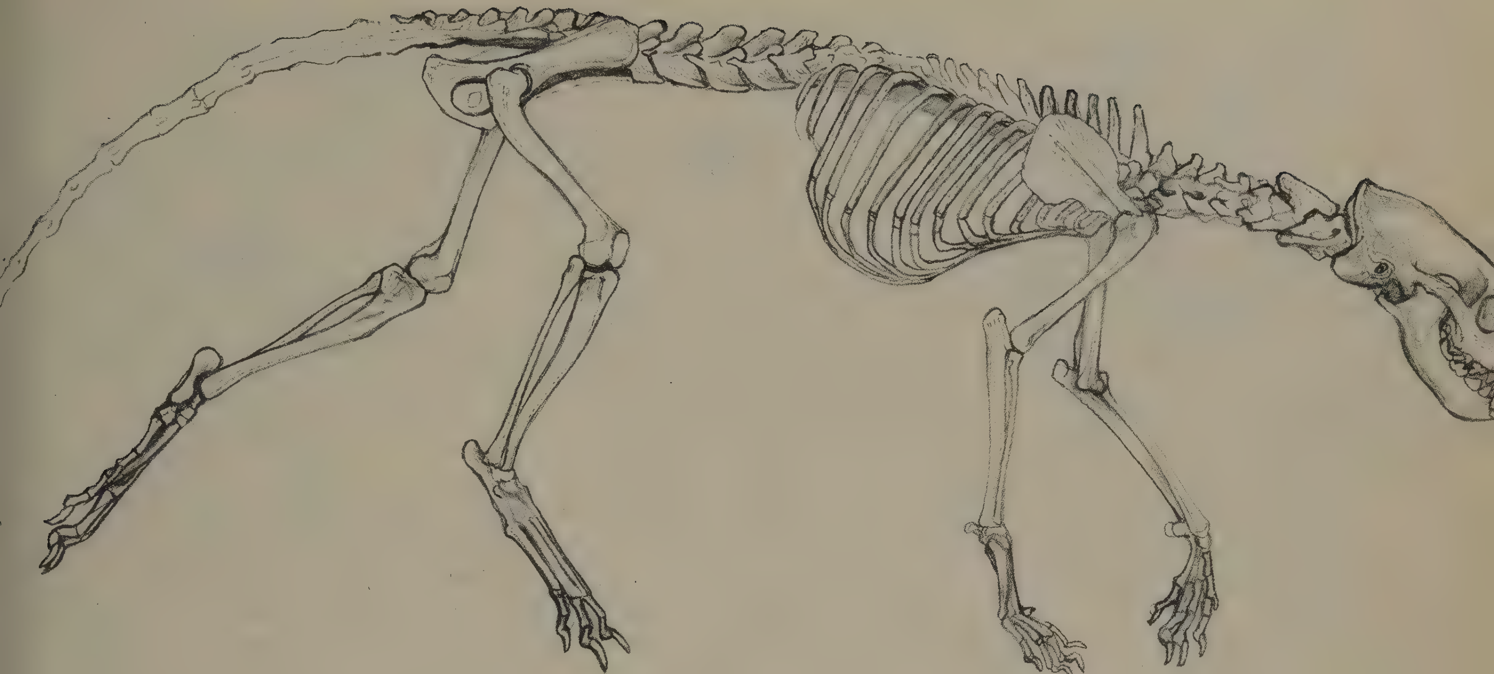
Freshwater crabs, mussels and snails are major foods, reptiles and birds and their eggs, large insects and their pupae or larvae, millipedes and various fruits have also been recorded.

These mongooses investigate every hole and crevice along river banks often extracting hidden crabs or frogs. When investigating ponds they patiently and systematically work their hands through the mud and water ahead of them while they take their weight on the hindlegs. The animal does not look at what it is doing, often holding its head well up in deeper water to avoid submerging it. However, the sifting motion is rapid and the dredging ranges back and forth through a pool again and again. If food is found, the item is usually pulled up out of the water and may be taken relatively slowly into the back of the mouth, the head tilting sideways to get a good purchase. If the prey is struggling actively a chewing bite with the front of the mouth will dispatch it and it may then be taken out on to a bank or tussock to be

Atilax paludinosus

eaten. I have seen favourite eating-rocks on an island in Lake Victoria, where mussels and crabs had been broken by being hurled downwards from a standing position. This modification of the usual mongoose throw was first described in detail by Steinbacher (1939) and it probably derives from the animal's rearing stance when it first raises food out of the water with its paws. Any hard object, mussels, crab, eggs and in captivity even stones are hurled down with considerable force (see drawing).

I was provided with an interesting insight into the innate nature of this animal's feeding behaviour when I came into possession of an adult female caught in a papyrus swamp in Buganda. Initially she retreated into her hutch with food, but after some months she took to rattling her empty drinking-dish for an hour or more before her regular feeding time. This was not, as my children insisted, ringing the dinner bell, but was due to her having come to associate the dish with water. It had served its purpose as a drinking vessel for a month without being touched or upset, but, once it had been identified as the only source of water in her run, it no longer mattered whether the dish was full or empty. It became a releaser for the full food-hunting action and she would scrabble and sift along the dented bottom of the bowl with the correct forwards and backwards motion. Eventually she would drop food items in her water, but only after taking the edge off her hunger. Ewer (1973) also saw a captive dowse items it did not greatly relish and interpreted the "capture" in the water dish as a facilitation of eating. I prefer to regard hand-sifting as a motor pattern finding expression *in vacuo* when the animal has been without food for some time and dowsing also as an innate food-hunting behaviour finding release once hunger is less pressing.



The marsh mongoose is also opportunistic about food and will hang around fishing villages for offal. I once saw one sitting quietly watching a fish-eagle, *Cuncuma*, that was perched directly above it devouring a fish it had caught; the bird's excreta showed that it regularly used this perch. Once, when netting waterfowl, I left a net unattended and returned to find a mongoose had killed and partially eaten a white-backed duck in the meshes.

Marsh mongooses are regular in their habits and follow pathways that are often surprisingly smooth and well-defined. It is possible that the sensitivity of the animal's palms influences this habit. While skinning one I discovered numerous small thorns embedded in its soft pads, illustrating how they are likely to be more susceptible to damage than most mongoose paws.

Their pathways tend to follow rivers or shorelines, often in the lee of grass or reed clumps and their tracks in the mud are a common sight along most East African streams.

The marsh mongoose has been widely credited by local people with employing a very bizarre subterfuge to catch birds. The story would seem quite outlandish were there not corroborative evidence for the behaviour pattern, even if not for its alleged purpose. My captive female occasionally would sun-bathe lying on her back, in which position her pale pink anal area assumed a quite startling prominence against the surrounding fringe of dark fur. This display is claimed to induce birds (including the locals' chickens), to approach and peck at the anus, whereupon the mongoose seizes the bird. This story was given further currency by Pitman (1951), and

in 1952 an eye-witness account by an honorary Game Ranger of Uganda, M. S. Tweedale, was published in the Uganda Game Department Report.

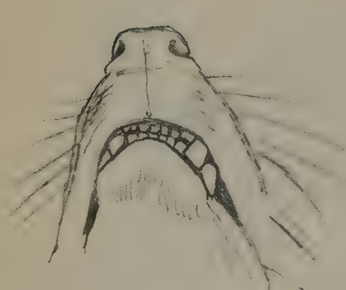
> "While waiting for crocodiles to come out on a sand bank he happened to glance around and noticed what appeared to be a dead mongoose on its back with all four legs in the air. He did not approach it as he did not want to startle the crocodiles who were about to come out on the sand bank. Suddenly a large brown eagle swooped on the supposedly dead mongoose. The bird then rose two to three feet in the air and fell to the ground. The mongoose immediately got up and was starting to carry it away when Mr Tweedale decided to investigate. As he approached the mongoose ran away. He found that the bird had had its throat bitten out. The animal was a water (or marsh) mongoose, *Atilax paludinosus*."

The mongoose might simply have been asleep but if it had been taken entirely unawares it does seem extraordinary that it should kill the raptor quite so effectively and then promptly carry it off. Further observations and perhaps even controlled experiments might help to explain the meaning of such behaviour. There are sufficient resemblances between this incident and the well authenticated behaviour of *Herpestes ichneumon* (p. 179) for it to be given serious consideration. Racoon-like behaviour and a diet of aquatic invertebrates have become the hallmark of this species so that killing of birds might represent an older feeding pattern. What Mr Tweedale saw could have been relict behaviour in *Atilax*, indicative perhaps of the more generalized carnivorous habits of this mongoose's ancestors.

In connexion with the neck bite, I once saw a marsh mongoose attacked by a dog get a grip on its opponent's throat and although one limb was being chewed it managed to get its squirming body over the dog's head. The weight of the mongoose threatened to drown the dog in less than a metre of water. Meanwhile it ejected jets of a foul brown fluid from the anal sacs. It is evident that these mongooses are well able to take care of themselves.

When a captive is approached by a dog or threatening human it makes a low growl, which may be reinforced by sudden explosive barking growls in a deeper key. When the animal is nervous the nictitating membrane and corners of the swivelling eyes are very much in evidence and when really cornered in a cage and distressed it urinates, exudes its creosote-coloured secretion and tries to curl up in a ball turning round and round and putting its head between its legs in a similar manner to that described by Rensch and Dücker (1959) for the Indian *Herpestes edwardsii*.

Like *Ichneumia*, *Atilax* has been heard to make a high-pitched cry and an open-mouthed bleat when excited (Michaelis, 1972) and I have heard a captive female sometimes utter a peculiar moaning call.



When seen out of the water, their silhouette is very characteristic and they generally walk rather deliberately. If frightened they make for the water, where they may swim away with the head and part of the back out of the water or dive, and they have been reported to stay submerged with only the nose above water (Sclater, 1900). When alerted, they often adopt a tall, tip-toe stance and very occasionally rear up on their hindlegs to peer round, sampling the air with sniffs.

The dung of marsh mongooses is deposited at dung sites on open areas, generally near the water's edge. In papyrus swamps I have found them on floating mats of well trodden vegetation that are clearly visited with some regularity. Around Lake Naivasha scats betray that mongooses now feed almost exclusively on the introduced Louisiana crayfish and they are also killing young coypus, likewise a species of recent introduction.

Marking with the anal gland is conducted in a hand-stand position which is evidently well adapted to a boggy habitat. The male is more prone to mark than the female (Ewer, 1973). The cheek or genal vibrissae have a secretion at their base, which Michaelis (1972) describes as smelling like honey. She also describes the mongooses as marking their own body without specifying how. The cheeks rub on the body during long self-grooming sessions, but this seems incidental whereas they are deliberately rubbed on objects by captives. Possibly the glands play a similar warning role to that demonstrated for *Helogale* by Rasa (in Ewer, 1973).

Most frequently seen singly, they are well-spaced along their generally linear habitat and are undoubtedly highly territorial. A mongoose that had dug its burrow near the lakeshore home of A. Root was once seen fighting and threatening another mongoose some 20 to 30 metres from the entrance of its den; the contestants were noisily bark-growling at one another. On the evidence of footprints activity appears to be fairly intensive in the vicinity of a burrow and although an individual might use several shelters these are seldom far apart and an animal's range in a favourable habitat is unlikely to be very large, although seasonal changes and less favourable habitats might make a great difference to the area used by one animal. I once saw a mongoose dredging small pools in a dried up riverbed in the middle of the afternoon. Feeding conditions had probably deteriorated badly over a prolonged drought, but the superabundance of tracks over a small stretch of river suggested that the mongooses' response to food shortage was to prolong its feeding periods and use its range more intensely, rather than try to extend its range into what were probably equally impoverished territories of neighbours further up or down the river.

It has been suggested that their vision is night-adapted and improves at dusk (Michaelis, 1972) but when they are active during the day they show no signs of disability. Although their underwater hunting is purely tactile, wild mongooses frequently submerge and it is possible that the eyes are somewhat adapted to regular submersion. A trapper told me that two of these animals that he had kept in a cage with no dark hutch and no more water than a drinking bowl had developed severe eye disease.

Although they are probably subject to various diseases, these have not been investigated. Loveridge (1923) listed various parasites. Didier (1948) noted the male's unusually long, thin baculum but very little is known of their sexual and social behaviour. Verheyen (1951) stated that they breed twice a year in Upemba, once in the middle of the dry season and once in the rains, the female apparently preparing a litter of dry grass in the hole or shelter. In some of the more extensive swamps it is evidently impossible to dig a hole or find a natural one and in these circumstances the young are born and raised in the swamp, perhaps on what Woosnam (in Shortridge, 1934) described as a nest of reeds, grass or sticks which floats in the middle of the thickest reed bed. In central Tanzania I found a female with her quarter-grown cub in early June and large foetuses were recorded by Loveridge (1923) in August.

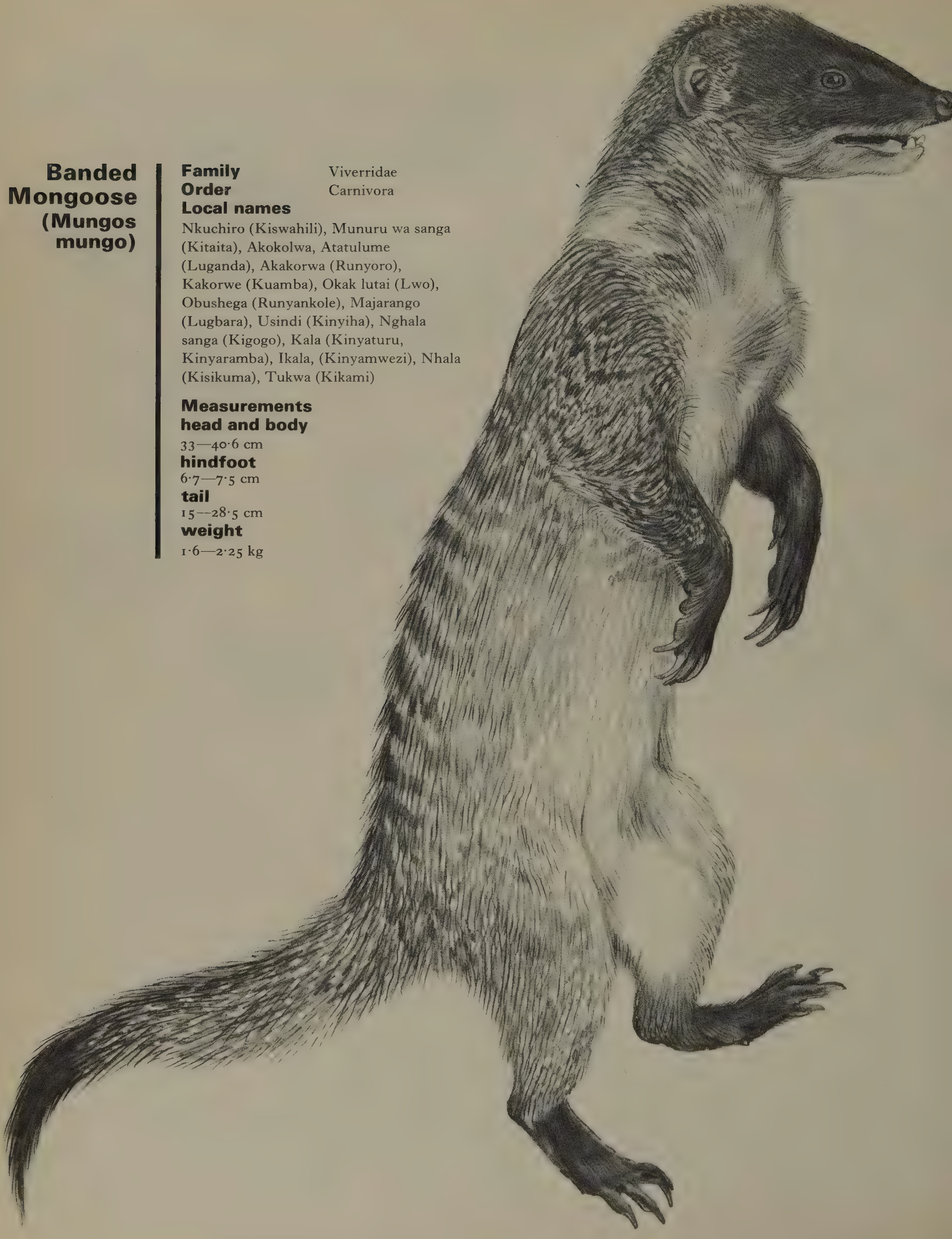
Up to three young have been recorded and one to three pairs of mammae, although it seems only one pair are truly functional. The young accompany the mother while still quite small; sometimes a second adult also accompanies the family and Fulton (personal communication) saw two adults searching for food with two young. Whenever an adult caught anything, the two little ones rushed up to share it. When one of the babies fell into a deep pool, it shrieked and was immediately pulled out by the mother. Verheyen reported his trappers' assertion that the young depart from their birthplace after a few months.

Atilax become very tame, particularly when caught young, are clean and easy to keep.

Banded Mongoose (Mungos mungo)

Family Viverridae
Order Carnivora
Local names
Nkuchiro (Kiswahili), Munuru wa sanga (Kitaita), Akokolwa, Atatulume (Luganda), Akakorwa (Runyoro), Kakorwe (Kuamba), Okak lutai (Lwo), Obushega (Runyankole), Majarango (Lugbara), Usindi (Kinyiha), Nghala sanga (Kigogo), Kala (Kinyaturu, Kinyaramba), Ikala, (Kinyamwezi), Nhala (Kisikuma), Tukwa (Kikami)

Measurements
head and body
33—40·6 cm
hindfoot
6·7—7·5 cm
tail
15—28·5 cm
weight
1·6—2·25 kg



Banded Mongoose (Mungos mungo)

In spite of belonging to a family of mostly solitary species, the banded mongoose is one of the most highly social of mammals. To encounter one on its own can only be due to a mishap; its proper place is amongst a scatter of grunting gleaners in the leaf litter or in a skirmishing line returning to sleep together in a packed mass of bodies in the den.

Superficially, it is in many ways a nondescript little brown carnivore but I remember the species assuming a special interest when I first saw a small pack of this mongoose display against a serval cat. So united and so integrated was their behaviour that they advanced in a writhing, spitting clump on the increasingly nervous cat. I saw the same group put an aggressive Alsatian to flight, biting the dog's heels as it fled.

Mungos mungo

I believe that central to this behaviour is the role of the animal's boldly striped rump and back and it is with a discussion of this aspect that a profile of the species can begin.

A small pack of wild mongoose once took up residence in my garden and during the wet season invaded the garage, where they dug a burrow under the cement floor. At that time I had a block of solidified yellow ochre pigment lying in their corner, and this landmark, like every other stone or lump in the vicinity, was marked with the anal glands. Soon each animal had a yellow back and this was due not to the mongoose rubbing its own rump on the pigment but to having its fellows rub their anal glands there, thus transferring the pigment onto the striped area of the back and base of the tail.

The banded hairs on the back are arranged so that they fall into lines instead of the agouti grizzle that covers the rest of the body and is usual in the mongoose. The effect of these stripes on another striped mongoose can be illustrated from my field notes: one mongoose was standing at right angles to another and about a metre away when it suddenly flopped down and rolled on to its side, turning its back on its fellow. With this sudden display of stripes the other mongoose instantly went forward and started marking the other's back, although the back was now in a poor position for the marker, which had to slew its pubic region to the side to get at it.

After the slightest separation or after a mild scare, these mongooses will often pile up on one another and, while they utter a warbling chitter, rub their glands on one another's backs. The same tendency is displayed whenever some new or rather dangerous situation is encountered, as when a stretch of open country or road has to be crossed, but at such times the action is obscured by continual movement. It is very noticeable in hand-reared tame ones which get constantly kicked as they try to touch or briefly mark the moving boots of a person crossing a field. Fiedler (1957) remarked on how the more a tame *Mungos* was handled the more it marked objects, and how marking was provoked by the visit of strange humans, a behaviour that is familiar to those who have watched or kept these animals.

Cantle (in Simpson, 1964) introduced two tame *Mungos* to three wild ones, whereupon they scent-marked the latter very strongly. Likewise, when

a pack of mongoose move back to a neglected den after an absence, they spend much time dragging their glands all round the entrance and mark repeatedly all neighbouring stones and stumps. Probably all mongoose species mark and re-mark objects in their territory, particularly if they are unfamiliar, but *Mungos* also scents his fellows and is unusual in having a visual target for the marking behaviour, which is elicited by an unusual or unfamiliar happening. Apart from its obvious function as a social adhesive, this behaviour has developed still further, serving these vulnerable little animals well in their invasion of the open savannas of Africa with all the attendant exposure to predators. The incidents with the serval cat and the dog were not isolated or unusual, and I have been able to see every grade of reaction, from temporary and desultory bunching with gentle rump-marking in response to a slight scare, to the full amalgamation of a pack in response to a large predator. The components of rump-marking remain the same but at the highest intensity the entire group are spitting and coughing as they writhe about dragging their glands feverishly over one another's backs and gaining confidence as they advance. The front ones may even rear up on their hind-legs to make little snapping lunges at the enemy, while the others surge forward, passing under one another and coming up under the others' forelegs; the effect is of a menacing monster relentlessly advancing as it rears its many heads. Directed at all sorts of animals, this behaviour can evidently serve both to frighten off predators and to clear the foraging area of competitors, and even harmless animals that could at most be no more than a distraction. In the Ruwenzori National Park, Rood (1974) saw bunching directed at herons, geese and the greater grey mongoose, *Herpestes ichneumon*, as well as raptors and marabou storks. He saw the harmless but numerous bushbuck attacked very frequently, having their hocks nipped until they left the current area of mongoose activity.

It is unlikely, of course, that the secretions of the anal sacs and the accessory glands carry the same information for the mongoose at all times, and Simpson (1964) has observed that

> "when the female is in oestrus the anal scent glands of the male become enlarged and the white secretion is produced in large quantities. During coquette the female becomes well covered in this secretion."

During courtship, the female also marks the male's back and there is no doubt that at all times both the pasting activity itself and the resulting scent are rewarding to all classes of mongoose, giving them assurance and in many contexts resolving tension.

In dry weather the scent is much less pungent and at this time a patch of damp ground or grass may provoke a paroxysm of marking and body rubbing, indeed water on a hot day may be more welcome for its scent-enhancing properties than for slaking the thirst. I often saw them moistening their fur before drinking, accompanying fur wetting with chittering, bird-like calls that generally signify a rewarding experience, such as the acquisition of a choice morsel of food. However, the anal scent marking was accompanied on these occasions by intensive cheek rubbing, which is emphatically an aggressive action, generally preceding biting in captives. Food, in fact,


bunching for attack
one mongoose
marks another
back

elicits the only serious aggression within the pack and their reaction to an ambiguous object is interesting.

Occasionally, if a mongoose encounters a smooth stone that has any resemblance to an egg, it may be clasped momentarily in the forepaws and then, instead of being hurled between the hindlegs, it is passed down to be marked by the anal glands. This excites the interest of other mongooses and each animal marks it. Finally, the animals may squat over the stone and tread their hindlegs up and down. This seemed to me to squirt the secretion actively instead of just wiping it, but by the time others had wiped their cheeks, throats and bellies on the stone, I was no longer able to ascertain if the anal sacs had actively extruded secretion. Dung may also be given an additional bouquet by being squirted with the glands, as the animals sometimes tread their legs up and down while defaecating on bare ground in the vicinity of the den. Several animals often do this simultaneously, after which they visit one another's dung and drag their belly or throat over the spot—the resulting scent of the mongoose is very strong indeed, but I think it is significant that I only saw this behaviour in the dry season, when the dung itself did not smear their coats. Simpson (1964) saw them play with the pellets of a hartebeest and, after rolling them around, rub their bodies against them.

After eating an egg or some other favourite food that has left a strongly scented residue, a mongoose will often rub its cheeks and throat about on the place and neglect to use its anal glands. According to Ewer (1973), displays of aggression follow chin-rubbing and this is probably associated with cheek glands. It seems that among the battery of scents available to *Mungos* there are repellent messages to counter or augment those of the anal glands which, at least to the members of a single pack, seem to be overwhelmingly attractive. The mixing of anal and cheek markings, particularly near the den, might therefore be directed primarily at strangers.

Although a *Mungos* pack always hunt socially, sometimes subdividing into smaller groups for a while, each animal is on its own as far as food is concerned, Simpson (1964) reported seeing a pack kill a large snake, *Psammophis*, in concert but the killing may have been as much an attack on a predator as on prey. Likewise, Rood (1974) saw a pack appropriate a hare from a fish-eagle and also drive vultures off a dead gazelle and then leave it alone. However, their predominantly invertebrate foods are too small to be effectively shared, and each animal is intensely possessive of anything it finds, eating it as rapidly as possible. Even if the prey is alive no time is wasted on killing it and Lammergeyer (1962) reported a 20-cm night adder, *Causus rhombeatus*, being eaten alive by a *Mungos*, which started at the tail end and continued until the snake was finished.

Termites, the most widely distributed of insects, are everywhere an important part of the mongoose's diet, but they generally rely on somewhat larger invertebrates; chief among which are millipedes and grasshoppers, earthworms, beetles and their larvae. Other important foods are crabs, scorpions, slugs and snails, lizards, small snakes, reptile eggs, rodents, shrews, ground birds and their eggs and fallen fruit. In the striped mongoose's savanna habitat many beetle, millipede and termite species flourish in the dung of herbivorous animals, and it is for this reason that striped mongoose are often common in rangelands and spend much of their time going from one turd to another. In the woodlands and gallery forest, a rich but well dispersed invertebrate fauna exists in the leaf litter and this too is exploited by *Mungos* in the more easterly part of its range. (In Uganda, the forest niche is mostly occupied by *Crossarchus*.)

While searching for food each animal sniffs continuously and turns over any moveable object beneath which food might be found; if a mongoose is brought into a house this habit can have destructive consequences. Scratching is very frequent and, once a food object is found, it is often dispatched with quick snaps and chewed up. Often, however, the object is rolled and patted very rapidly, the mongoose meanwhile goes backward taking small sampling bites. The highest intensity of rolling and patting is reserved for slugs, snails and toads, where the action provokes and eliminates some of the defensive slime that these animals exude. Any egg that the mongoose finds is also scratched back between the legs, an action that usually succeeds in breaking it. Should the egg be hard-shelled the movements become more vigorous and the egg is hurled violently through the hind legs. Young captives do this quite instinctively but the throwing is without direction and it is only experience that teaches them the need for a hard object to throw against. An egg given to a mongoose in an open field is eventually dribbled

Mungos mungo

expertly to the nearest stone or tree trunk and smashed. The same behaviour is followed with pill-millipedes (see Eisner and Davis, 1967).

Apart from needing abundant food all the year round, *Mungos* needs shelter at night. Although quite capable of digging a burrow when necessary, they seldom have to do this and use termitaries, rodent holes or natural crevices, which they may modify.

The burrow may be changed from time to time but they usually seem to have favourite dens to which they return many times, often choosing to breed there.

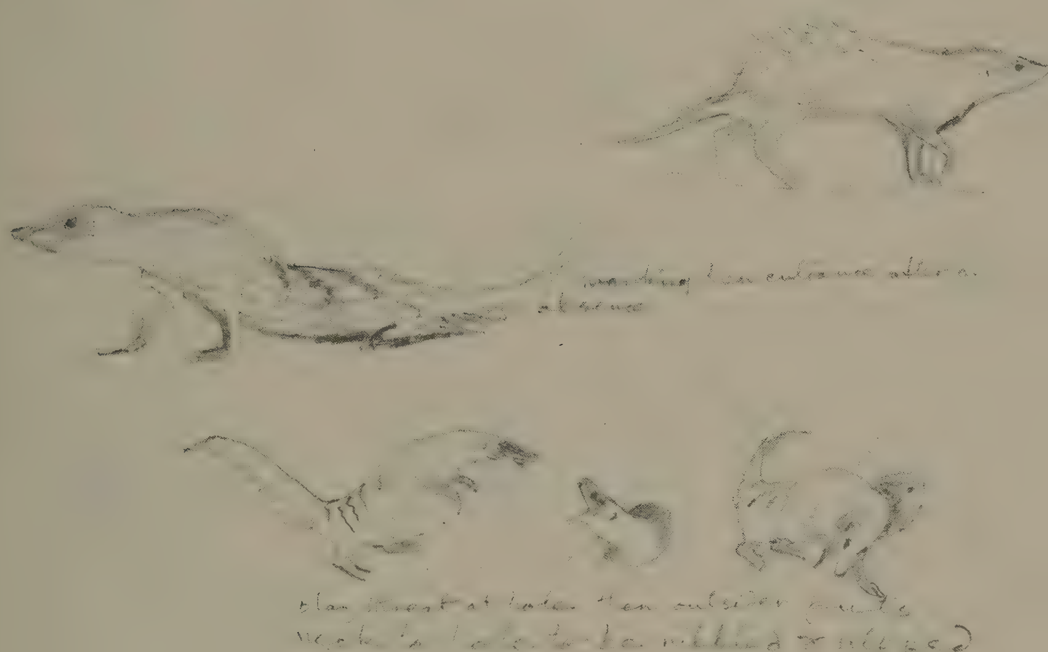
Verheyen (1951) reported the female collecting nesting material and Simpson (1966) described the young being born in a grass-lined chamber but there is no evidence of the other members of the pack furnishing their den. However, a captive used to block up the entrance to its box with a blanket at night (Dalton, 1961). They usually return to a den before nightfall and after a rest outside go down as it gets dark. On two occasions I have seen them about in bright moonlight at about 9 p.m. in dry weather. The first animals start to emerge at about 7 a.m. depending on the weather and they come out later on wet, cold days; likewise they may return an hour or two earlier on such days. Feeding continues throughout the morning, after which there is a long resting period during the heat of the day, often under dense bushes. This is often accompanied by much play, chasing and wrestling and some individuals may mark one another's backs and stay for long periods in what looks like a copulatory position. Sometimes they may bask or doze in the sun but will start feeding again if it goes behind clouds. Neal (1970b) describes a pack that he ambushed before nightfall:

> "Having waited there until it was nearly dark, they then made a concerted dash for the den, looking from a distance like a single, large, dark, sinuous snake as they ran close together, head to tail."

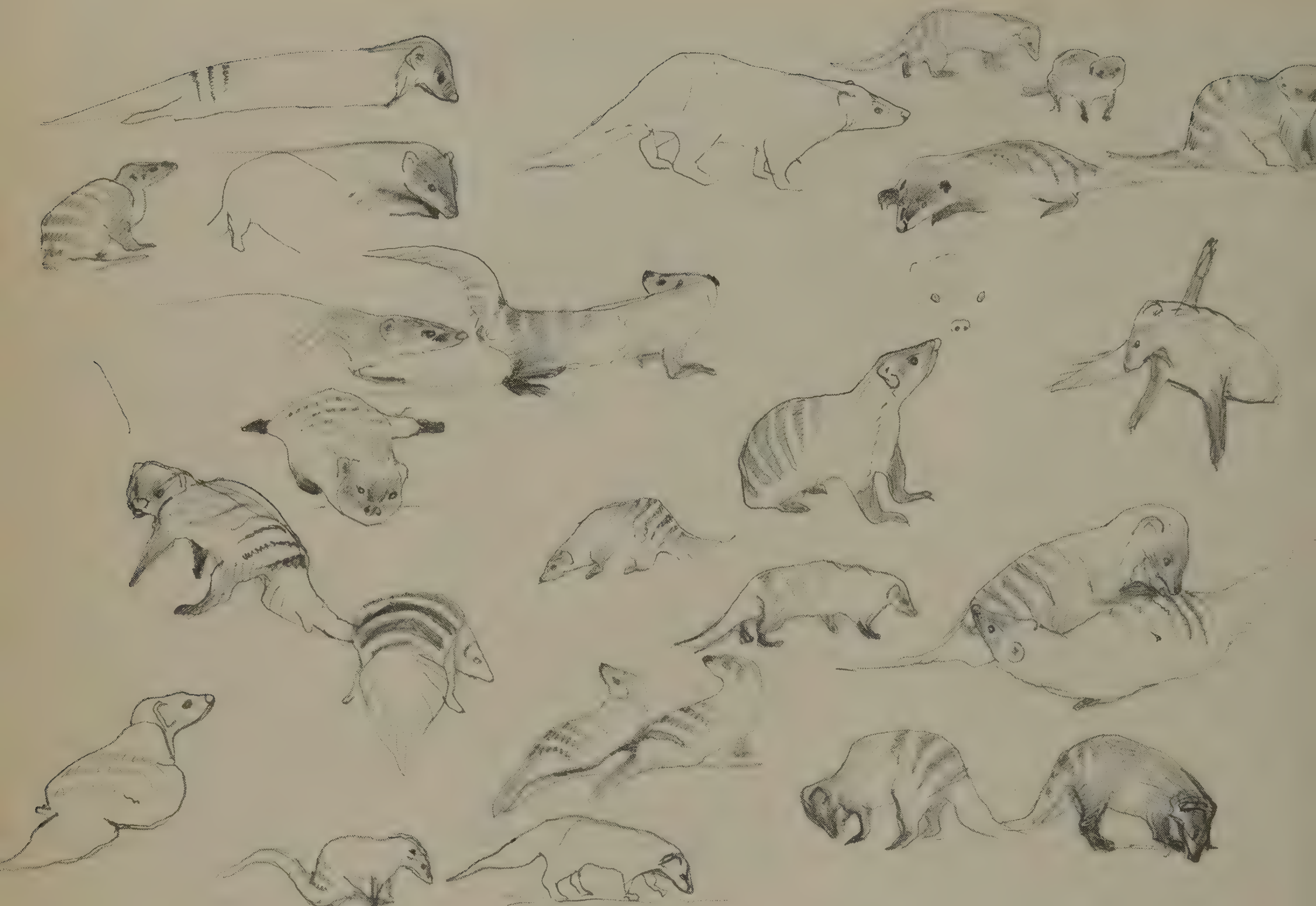
On the rare occasions when an individual gets lost and out of earshot it tracks the pack down by scent. While foraging, each member of the pack punctuates his activity with a short, single grunt, so that the whole pack is

webbed by sound, even when quite scattered. A chattering from any individual alarms all the group and mongoose rising up on their hindlegs with their hair smooth elicit silence and attention in the others which also tend to stand up and look around. Flat hair, which emphasizes the stripe pattern, is always associated with alarm or stress. The pack will tend to bunch in these circumstances with the young getting into the middle of the group and they make for the nearest shelter.

The pack is a closed group in which the sexes are about equal in number and status. Total numbers range between 4 and 40. There are very marked differences in the degree of boldness or timidity of individuals and dominance



seems to be relatively independent of sex. The dominant animal bites at the back of another's head but this can turn to nibbling which the inferior animal gives every sign of enjoying. I have seen a female mongoose blocking the entrance to a hole being playfully threatened by another female outside. The one in the hole responded with gaping jaws and some feinting took place, but when the one in the hole withdrew, the other deliberately put her neck in the hole to be bitten—the sequence was repeated many times, the mongoose outside sometimes rising on her hindlegs and raising her tail at the same time. Playing at the entrance of a burrow is very common and the excluded animal often leaps forward and then goes backwards fast, furiously scraping earth, leaves and sticks with its claws, only to pounce forward again. Dragging vegetation is an aggressive action and a dominant animal may use its tail to stir up leaves while moving in either direction. Changes in the status of individuals can take place, as was well illustrated after a car ran over a



dominant female in a small free-ranging group, damaging its back and causing it to drag its hindlegs. It was subsequently attacked by the others whenever it found food anywhere near them and it would probably have died had we not fed it after distracting the others. Once it had recovered it was accepted again but it never regained its former dominance.

A subdominant animal will either run away or sometimes try to fight over its shoulder, meanwhile presenting its rump to the aggressor. I suspect that this gesture counters the aggression with an attractive signal—the stripes—but in contrast to the bunching context an appeasing mongoose keeps its fur bristling.

Forty animals in a pack seems to be the maximum size and Shortridge (1934) noted that an unusually large colony divided into several troops which hunted independently. Rood (1974) has watched the culmination of this splitting:

> "New packs appear to be formed by a few adults separating, apparently voluntarily, from the parent pack. These may stay within the pack's home range for several months. The amicable relationship normally occurring between pack members is gradually lost and the members of the new pack are eventually treated as strangers and subjected to aggression. Eventually they may move or be forced out of the original range."

Ranges vary enormously; presumably the food resources determine this. In Ruwenzori National Park, Rood found a mean home range of 80·4 hectares. In Serengeti he found troops ranging over 4 sq km (personal communication).

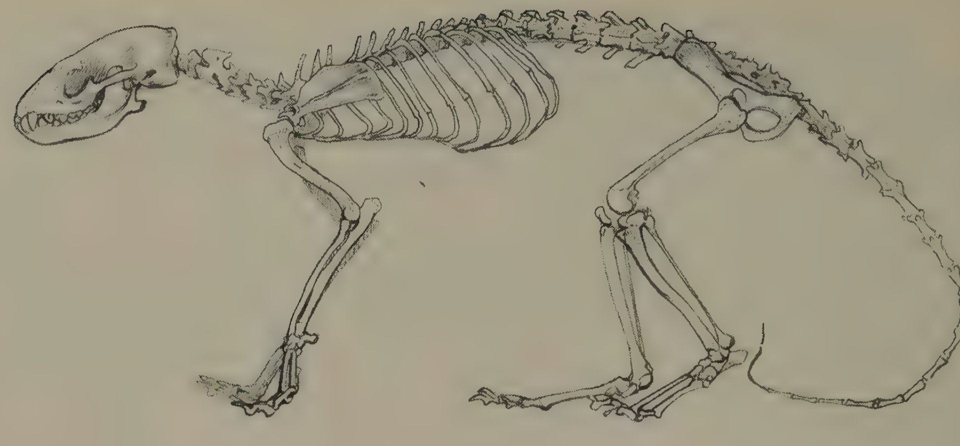
The size of the pack is of some import in settling encounters between different packs and Rood (1974) noted that equal sized packs fought most intensively:

> "The mongoose packs did not appear to be defending specific areas during aggressive encounters. The sight of a neighbouring pack was sufficient to release aggression and a large pack at the edge of its range could cause a smaller one at the centre of its range to retreat."

An encounter between packs is a very noisy affair with much screaming and chirring and a great deal of chasing, fighting and anal scent marking. In contrast to the predator reaction, the packs often disperse widely as individuals or small groups chase one another. They also fluff out their fur. Sometimes one pack goes to ground, and Rood described how the males of a larger pack scratched and scent-marked around the den of a grounded pack and remained there for over three hours. They eventually left, whereupon the other pack emerged and left in the opposite direction.

The number of females producing litters in a pack is, according to Rood (1974), independent of the size of the pack. In the context of restricted breeding in *Helogale* packs it would be very interesting to know what behavioural and physiological mechanisms control the inhibition of breeding in the sexually mature females of social species of mongoose. According to Simpson (1964) ability to conceive is reached at the age of 9—10 months. Rood found that within a pack several females synchronized their births but he noticed that neighbouring packs followed different cycles so that social, rather than environmental stimuli, must be controlling breeding. Although there may be up to four litters in a year, Rood found that peak birth periods were correlated with the rains in the Ruwenzori National Park and he observed that a mating period frequently begins in a mongoose pack a week or two after the birth of young, at which time most of the sexually mature females become receptive. In courtship a male chases a female at first and circles her with his tail held high; Neal (1970b) saw them face up as if for sparring and then chase round in tight circles which finally led to mounting. Copulation can last for up to 10 minutes and the female may be mated by several males one after the other; each of them smears her back with secretion and indulges in much nuzzling and rubbing for the six days she is in oestrus. Rood (1974) saw females mated by males from foreign groups during pack clashes and suggested that this might be a mechanism against inbreeding.

Gestation is in the region of two months and two to six young are born at a time and they are suckled by any lactating female in the den. At birth



they are blind and helpless and very small (head and body 100 mm; tail 40 mm). Nonetheless, their birth has no effect on whether the den is moved or not, and Rood (1974) occasionally saw a pack with young move their quarters daily; the young are carried by the scruff of the neck or by a random mouthful of folded skin. Rood (1974) has described in detail how males play an important role in guarding the young before they begin to accompany the pack. Generally a single animal but sometimes up to six may stay behind while the rest of the pack forages. Sometimes away for the whole day, packs with young usually return at the end of the morning and subsequently forage in small groups. According to Rood's observations, adult males guarded 29 times, non-lactating females 18 times, the mothers 10 times and juveniles three times. At first only joining the pack for afternoon excursions, the young travel with the pack all day when they are about 5 weeks old, by which time they have lost their dark colouring and have similar colouring to the adults. In the Ruwenzori National Park, where there is plentiful cover, less than 50% of the juveniles recorded by Rood survived to the age of 3 months, whereas adults—over 6 months old—showed an annual mortality of only 10%. Both these percentages are likely to be higher in more open habitats.

Not all predators are impressed by clumping and the following report is an interesting example of a situation in which it is not clear whether a pack influenced the predator's reaction or not, but their staying on the scene must have assisted escape, once the victim was released.

> "A martial eagle was observed to swoop on and catch a banded mongoose out of a colony which were grubbing about on short, green grass. The eagle flew to a nearby tree, with the mongoose in its claws protesting loudly. The entire colony followed the bird and screamed and chattered under the tree. The captured mongoose must have put up quite a struggle, as the eagle suddenly dropped him, and he ran off with the rest of the colony." (T.N.P., 1958)

Mongooses seem to discriminate between their enemies, however, and

Cantle (in Simpson, 1964) reported seeing banded mongooses climbing into the branches of a felled tree to escape a wild dog; in spite of being particularly poor climbers, this pack obviously recognized the inadequacy of their defences against these particular predators. It is interesting, however, that another pack—containing only four mongoose—should have put a large Alsatian to flight. Simpson (1964) reports lion and leopard also chasing these mongooses but notes predatory birds as their chief enemies. Even tame individuals retain a clumping response, rushing to their human protector's shoe at the shadow of a bird or the bark of a dog.

There is no information on diseases but they may be subject to rabies. Ansell (1960b) reported them becoming especially abundant in northern Zambia about 1956 and suggested that they might follow population cycles. Captives have lived nine years.

Long-nosed Mongoose (Crossarchus alexandri)

Family Viverridae
Order Carnivora
Local names
Andere (Kuamba), Kindere (Lubwizi), Sunsunyet (Sebei)

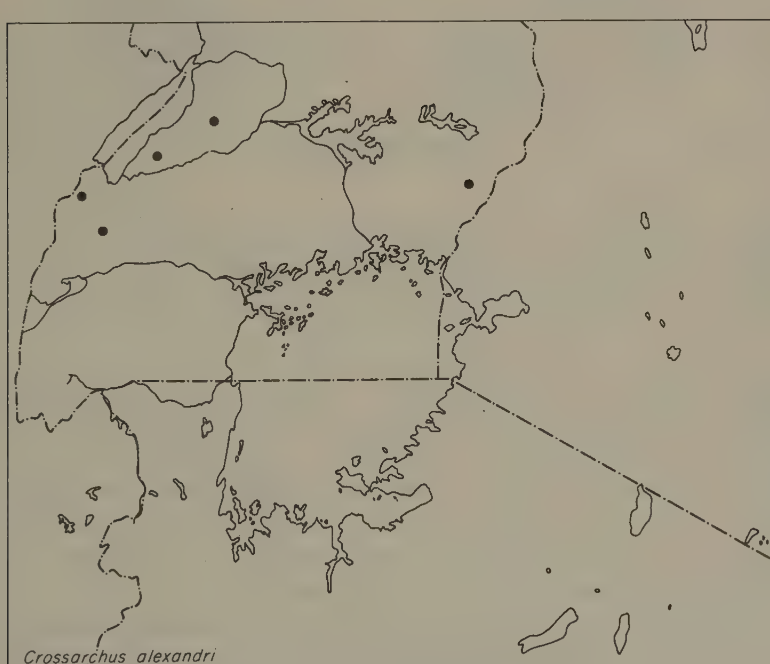
Measurements
head and body
36—40 cm
hindfoot
7·5—8·5 cm
tail
2·2—2·9 cm
weight
1—2 kg

Long-nosed Mongoose (Crossarchus alexandri)*

The pale short-furred face of this mongoose looks out as if from a shaggy black-brown cape. Its paws are sleek and black and there are long, sharp claws on the forefeet. The elongated snout is its most striking feature and it is adapted to probe into the soft and often swampy soils of the forest floor.

This mongoose is a Central Forest Refuge form but it has a less restricted range than some species, occurring in all the lowland forests between the Oubangui and Kasai rivers as far as West Uganda. It also occurs between 1,500 and 2,900 metres on Mt Elgon. Although the Mt Elgon population would appear to be somewhat isolated both geographically and ecologically, these animals are quite indistinguishable from those from further west.

This species lives in thick undergrowth and, in my own experience, prefers swampy areas. Aeschliman (1965) described *C. obscurus* as preferring the margins of lagoons and the vicinity of water, while Michaelis (1972) lists them living not only in montane forest but also in a semi-domesticated state around villages, and Ewer (1973) even saw parties of them on the Accra plain. By contrast, *C. alexandri* has not been seen near villages and seems to be a strictly forest-dwelling species (Rahm, 1966).



* It might be conspecific with the smaller West African *Crossarchus obscurus*, in which case it should be *Crossarchus obscurus alexandri* (see Coetzee, 1967).

Likewise, the foods of *C. obscurus* listed by these authors resemble those of *Mungos mungo*; vertebrates, invertebrates, snails and various insects have been listed. Booth (1960), writing of *C. obscurus* in Ghana says:

> "It is said that co-operative hunting has in this species reached quite a high pitch. The giant rat (easily as big as the *kusimanse*) is driven from its hole by one member of the party, who goes down after it; then the others pounce as it emerges. Normally, however, its prey is much smaller fry. I have found mice, lizards, insects and earthworms in the stomachs of shot specimens."

Four stomachs of *C. alexandri* collected in West Uganda, contained a sort of thick brown soup of animal matter and probably consisted of the well-chewed remains of slugs, snails and worms. One had eaten a beetle and a fifth was full of fermenting fruit. Rahm (1966) calls *C. alexandri* carnivorous and frugivorous but also mentions arthropods as food. On two occasions I have watched them rooting about in wet leaf-litter and soil.

The animals forage in a wide scatter like *Mungos*, but they push their noses into every crevice as they scrape and scratch continuously. Small

mammals were killed by Ewer's *C. obscurus* with a single fast bite on the back of the neck and she suggested that this betrays the more carnivorous habits of the kusimanse's ancestors. Naundorff (1936) found that a captive was able to find well-hidden food solely by following its nose. I have seen them climbing sloping trees while foraging and they are certainly more adept at this than *Mungos* is.

Like *Mungos mungo*, this species is a social animal and is also armed with glands. It has the habit of frequently standing on its forelegs to wipe its secretion on tree trunks and branches some 25 cm off the ground, and the structure of the anal gland is apparently well adapted to extrude secretion from a hand-stand position (Ewer, 1973). Marking with the cheek glands was never seen by Ewer without its being accompanied by anal marking, but she was unable to demonstrate a threatening function for cheek marking.

Captives tend to drop their dung and urine in one place and respond to the urine and faeces of other animal species by scratching and then superimposing their own urine or anal deposit. These mongooses grunt and twitter continually while feeding but any alarm excites a loud chatter, after which they run off in silence, except that they churn up leaves and twigs as they go.

C. obscurus is generally described as diurnal, but Ewer remarks that they also forage after dark and Naundorff (1936) termed the eyesight of his captive as good as that of a cat. Rahm (1966) says that *C. alexandri* is nocturnal but I have seen them active in the early morning, afternoon and evening. It is possible that in the forest undergrowth the distinction between day and night is less important than it is in the open.

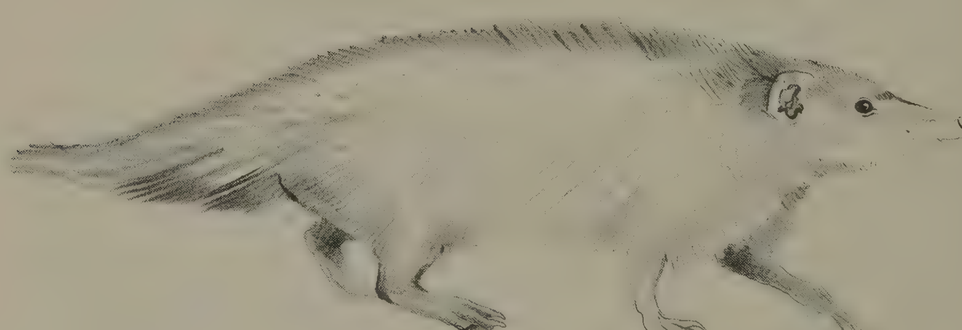
Vulnerable primarily because of its exposure, *Mungos* generally escapes nocturnal predators in its burrow. *Crossarchus* may be a lot safer in the undergrowth but it too takes shelter in termitaries or in hollow trees (Rahm, 1966) though it is also able to dig its own holes. Repeating the observation of hunters, Michaelis (1972) says that animals are seldom seen for more than a few days in the same place. Dorst and Dandelot (1970) claim that *Crossarchus* wander on a circular course, returning to the same place and Aeschliman (1965) claims they are faithful to a territory and dislike being displaced.

I have seen a pack of over 20 animals together and *C. obscurus* too is commonly reported in groups of this size. Ewer (1973) found her captive females were invariably larger and dominant over the males as far as access to food was concerned and she described their threat display:

> "The hair is fully erected, the back somewhat arched and the limbs much extended; the animal moves forward at a walk . . . it may alternatively move forwards towards the opponent and backwards away from him. The tail with maximum piloerection is held sloping downwards and at every step is swung violently from side to side so that, viewed from in front, it suddenly appears and disappears first to the left and then to the right of the almost globular body. Although to a human observer they may have a comic element, both performances are extremely impressive."

Fighting is stylized and directed at the sides of the neck behind the ears.

Single animals never groom themselves and get to look very scruffy. By systematically combing her pets, Ewer found that they moulted twice a year.



Her females had repeated heats when not pregnant and she concluded that *Crossarchus* is probably not a seasonal breeder.

> "The beginning of the female's heat may first become obvious by the males following her more closely and marking more frequently than usual. My male *Crossarchus* at this period behaves as though attached very literally to his partner: where she goes, he goes and where she rests he does. He also marks very frequently and becomes rather aggressive, especially towards anyone handling the female." (Ewer, 1973)

About four young are born to a litter and to date nothing has been published about their development or care.

Captive *Crossarchus* are favourite pets in West Africa and are very playful. Aeschliman (1965) watched six wild mongooses playing at tag in an open space in the forest. A party of *Mona* monkeys descended from the trees and took to pulling their tails and the mongooses flew at them with leaps and bounds. When pursued by dogs they have been reported to take to trees. Captives have lived eight years.

White-tailed Mongoose (Ichneumia albicauda)

Family Viverridae
Order Carnivora
Local names
Olunywamunte (Luganda), Okak ladolo (Lwo), Ekokwasi (Ateso, Karamojong), Sakaa (Kinyaturu), Kananga (Kikami), Waranyet (Masai), Usambaruo (Lugisu), Nueli (Luhya), Mwalasangali (Kitaita), Kalakonje (Kiliangulu), Kiihu (Kikuyu)

Measurements
head and body
53—71 cm
hindfoot
10—12·3 cm
tail
40—47 cm
weight
3·5 (2·6—5·2) kg

White-tailed Mongoose (Ichneumia albicauda)

Ichneumia albicauda

This slender long-legged mongoose usually has a conspicuous white tail but there are regions, notably the interlacustrine area of Uganda, where about one in three have black tails as well as an overall darkening of the coat. This non-melanic colouring is light grey on the face and body with long black guard hairs over the body and dark coloured legs. Superficially there is some resemblance with the ant-eating mongoose, *Bdeogale nigripes*, but the entire mien of the animals is quite different.

Widely distributed over most of sub-Saharan Africa it is absent from the more extensive areas of true forest, montane areas above 2,500 metres and from the driest parts of southern Africa and Somalia. It occurs in southern Arabia. It is strictly nocturnal in most areas but has very occasionally been seen out during the day. Its day-time retreats are natural crevices, old aardvark or pangolin burrows, termitaries or thick tangles of vegetation. It is commonest in country with an abundance of such shelters and this might influence its conspicuous abundance in some areas, without regard for vegetation type.

Common over most of East Africa, its very catholic diet allows it to make use of a variety of seasonally available foods. Flying termites, grasshoppers, dung beetles and their pupae and caterpillars tend to be especially abundant at times, while other insects, fruit, ground nesting birds and rodents are also more available at certain seasons. Examination of stomach contents has shown that a variety of foods may be eaten in a single night; thus various insects, fruit, scavenged carrion and small mammals or reptiles may all be present in a single stomach. Its main food, insects, are picked off vegetation or dug out of the ground or from piles of dung, beetles' pupae being especially favoured. In this connection it should be noted that the white-tailed mongoose is often common in areas with concentrations of ungulates, where it is frequently to be seen at dung hills or droppings, eating beetles or digging up larvae. Loveridge (1923) fed a captive the pupae of wasps and moths but noted that it ignored the grubs. These mongooses often come to street or house lights to pick up the moths and other insects attracted there and can be seen in company with jackals or black-necked herons that are also picking up dazed insects. They are fast but do not snatch at their prey and they are capable of killing animals up to the size of a hare or cane rat and have been seen chasing the former. Eggs are opened in the usual mongoose manner of hurling them between the back legs.

Snakes and other reptiles (including poisonous species), have been found in stomachs. Tarlton recounted to Roosevelt (1910) how a white-tailed mongoose was introduced to a two-foot puff adder.

> "Instantly the latter sprang towards the snake, every hair on its body and tail on end and halted five feet away while the snake lay in curves like the thong of a whip, its head turned towards the mongoose. Both were motionless for a moment, Then suddenly the mongoose seemed to lose all excitement, its hair smoothed down and it trotted quietly up to the snake, siezed it by the middle

Ichneumia albicauda

> of the back—it always devoured its food with savage voracity—and settled comfortably down to its meal. Like lightning the snake's head whipped round. It drove its fangs deep into the snout or lip of the mongoose, hung on for a moment and then repeated the blow. The mongoose paid not the slightest attention but went on munching the snake's body, severed its backbone at once and then ate it all up, head, fangs, poison and everything; it never showed any signs of having received any damage in the encounter."

Unfortunately, Roosevelt has also perpetuated Ndorobo folk tales that probably refer to the ratel rather than this mongoose, with which it has sometimes been confused. He reported that this mongoose is arboreal and a great killer of tree-hyraxes as well as a destroyer of beehives, none of which is true.

In Uganda, Pitman once lost some chickens to a white-tailed mongoose that bit their heads off when they peered through the wire. Sitting up to punish the offender, he describes what he saw in the following words:

> "The mongoose was behaving most strangely. It moved with dancing, jerky steps, slowly up and down the cage front, It bobbed up and down, raised and lowered its bushy tail, shuffled backwards and forwards, never for a moment ceasing its weird pantomime. No sound was uttered but the fowls presumably soon detected the intruder and in their foolishness got down from their perches to investigate, cackling all the while."

"Dancing" the tail is a common activity among white-tailed mongooses and connecting this activity with a deliberate luring of birds seems somewhat far-fetched, but in the light of similar observations of *Herpestes ichneumon* and *Atilax* such observations should not be dismissed altogether. Besides it should be possible to investigate the behaviour further as both mongooses and chickens are common enough.

Pairs of white-tailed mongooses can sometimes be seen, with one animal zig-zagging in front of the other with its tail erect and fluffed out. Tame mongooses often use the tail as a switch, flicking it against a human or canine playfellow, apparently as a provocation to chase, so it is odd that such a prominent feature in their behaviour should be so mutable, for black tails are hardly a conspicuous signal in the dark. In addition to its role as an intra-specific signal, the white tail might also be aposomatic, warning enemies of its distasteful smell. This species has a particularly nauseous secretion in the anal sacs but this is sometimes no deterrent to a pugnacious dog, so that advertising it might sometimes be disadvantageous. In the Makerere University area these mongooses were once very common but were virtually eliminated when a gang of watchdogs took to roaming the hill at night in search of sport. Likewise, within the limits of Entebbe township a known

total of 45 white-tailed mongooses were killed by three dogs in just over one year, a figure which gives some idea of the densities of mongooses possible in favourable localities. This species is a common scavenger in many villages and small towns.

Although normally seen in pairs or family parties, these animals sometimes join in larger groups. Watson (1950) reported seeing large numbers on Moroto aerodrome and I once encountered a group of nine, all apparently adult-sized and black-tailed, fanned out in short grassland, busily foraging but moving together in the same direction. They were feeding on dung beetle pupae and crickets.

This species is highly vocal and I have called one up to within a metre or two by imitating a whimpering call with which they appear to keep in touch. When digging they sometimes make a muttering noise and captives, when groomed or patted, utter a vibrating but rather guttural purr in short bursts. They growl when trapped, shriek if approached and scream loudly if bitten by a dog. However, their most unusual call is a rather dog-like yap or nasal bark. This explosive sound might be connected with sexual behaviour, for it is not heard throughout the year.

The swollen skull profile might be connected with this call, as both this species and *Rhynchogale* have large empty air sinuses in the interorbital area behind their nasal cavity, suggesting that these spaces might somehow give resonance to their call.

Although they have very occasionally been seen about during the day, this species is normally strictly nocturnal, spending the day in a cool retreat. They are most commonly seen from dusk until about midnight and again between 4 a.m. and dawn.

Information on mating behaviour has not been published but as two adults can sometimes be seen in company with subadults, it seems likely that pairs might associate for some time.

The few birth records available are inadequate to indicate any pattern of breeding. In central Tanzania, I trapped a female in September, which gave birth in her cage to four stillborn young, and Loveridge (1923) recorded foetuses in February. In Buganda, I collected a lactating female in June and I once saw a mother carrying a small baby out of a flooded drain in April.

The two to four young are born in burrows and are blind and thinly haired at birth. Popular as pets, the young are very playful and enjoy chasing games, dragging clothes to invite pursuit; they will throw somersaults when playing and indulge in much tail-switching.

Like other mongooses they are possibly involved in the transmission of rabies and they are known as a reservoir for rickettsia-borne diseases.

In the Singida area they are the equivalent of the black cat, a witch's familiar, while in Teso the skin is used by a formerly childless couple as a charmed blanket to protect their baby.

Meller's Mongoose
(Rhynchogale melleri)

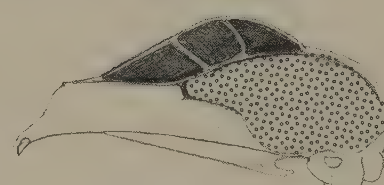
Family Viverridae
Order Carnivora

Measurements
head and body
44—48 cm
hindfoot
9·5—10·1 cm
tail
28—40 cm
weight
2·5 (1·7—3) kg

Meller's Mongoose (Rhynchogale melleri)

Rhynchogale melleri

In general appearance and body build Meller's mongoose is very similar to the white-tailed mongoose but it is yellowish brown with very long and coarse black guard hairs and a bushy tail, which is heavily outlined in black when fluffed out. There is a curious cowlick of reversed hairs along each side of the neck. The head has a number of peculiar features. The most striking being its short swollen muzzle, which is without the usual nasal crease on the upper lip, and a distinctly retrousse nose. The molars are broad and flat and the skull has a swelling above the orbits like *Ichneumia*. The swelling is due to empty sinuses which show considerable individual variation in size; nothing is known of the voice of this mongoose, but the hammer-headed bat, *Hypsignathus*, has sinuses in this region which are connected with resonance. *Ichneumia* has a loud nasal bark which is possibly enhanced by the possession of these hollows behind the turbinal area. An alternative but rather far-fetched possibility is that the sinuses are protective, giving a false "hull" to the top of the head (but only man is likely to direct a blow deliberately to the top of the head). Ansell (1965) noted a young adult with the intertemporal inflation developed to a remarkable degree and it is interesting to note that swelling in this region has been seen in the skull of a skunk, *Mephitis*, where



Cross-section of
nose in relation to skull

it seems to have been caused by disease. Apart from *Ichneumia* the swelling of the nasal sinus is very pronounced in one other viverrid, the binturong, *Arctictis*, which is also relatively short-nosed. This Oriental civet is very slow in its movements and like *Rhynchogale* is reported to feed mainly on fruit and carrion.

* = specimen records
stipple = principal areas where habitat might be suitable

Smithers (1966b) states that up to three young are born at a time and that births occur about November in Rhodesia.

Wilson (1968) recorded a litter in Zambia in December. The two young were male and female, had closed eyes and were found in a small cave on a rocky hill. A second record from this area was of a pregnant female also containing two young, one of each sex.

Further information on the biology of this species and an investigation of its specializations are needed.

Smithers (1966b) states that the diet of *R. melleri* consists of termites but the series in the British Museum collected by Whyte in Malawi was labelled "wild fruits are always found in the stomachs". Their habitat appears to be restricted to the woodland belt in south-eastern Africa but within this belt it is possible that they are restricted to the moister and more heavily grassed or wooded areas such as drainage lines and rock outcrops. The absence of

sight records may be partly due to their undistinguished appearance but it is also likely to be due to their keeping to thick cover and being very shy.

The biology of this species is entirely unknown. Records suggest it is nocturnal and solitary. Ansell (1965) reported two males found dead together and suggested they might have killed one another in a fight. Both were old with heavily worn teeth and had lost their last molars in both jaws.

Front legs and feet

Back legs and feet

B. crassicauda crassicauda

B. crassicauda omnivora

B. nigripes

Four-toed Mongoose (Bdeogale)

Family Viverridae
Order Carnivora
Local names
Ngogo (Kisambaa), Kitu (Kinguja)

Measurements

B. crassicauda crassicauda

head and body
40—50 cm
tail
20—30 cm
hindfoot
7·4—9 cm
skull length
8·2—9·2 cm
weight
1·5—1·6 kg

B. crassicauda tenuis and B. c. omnivora

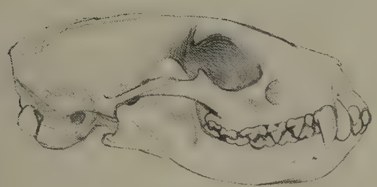
head and body
34—45 cm
tail
18—24 cm
hindfoot
7—8·1 cm
skull length
8—8·5 cm
weight
0·9 kg (estimated average)

B. nigripes

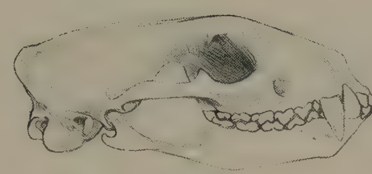
head and body
52—57 cm
tail
27—36 cm
hindfoot
8·2—10·6 cm
skull length
10·8—11·7 cm
weight
2—3 kg

B. nigripes

Four-toed Mongoose (Bdeogale)



B. tenuis



B. nigripes

B. omnivora

Species

Bdeogale crassicauda
Bdeogale nigripes

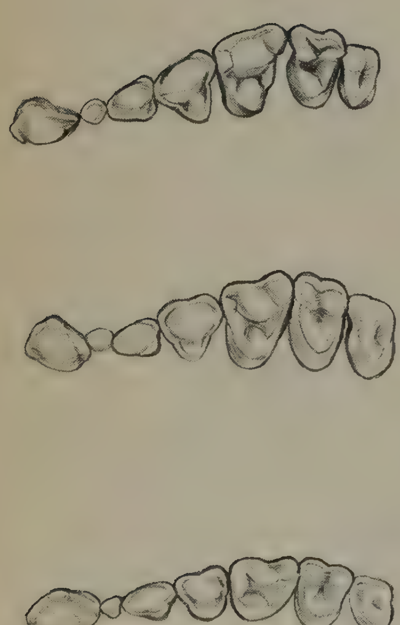
Bdeogale crassicauda. Smaller size (total length generally less than 75 cm). Long dark tipped guard hairs on back and tail. Short hair on exposed ears.
Bdeogale nigripes. Larger size (total length generally exceeds 80 cm). Short light-tipped guard hairs on body and tail. Woolly ears. The Kenya population has been found for the most part at high altitudes and has a thicker, longer coat and (possibly) smaller dimensions than the West African lowland populations. Should these differences warrant recognition at the subspecific level, *B. nigripes jacksoni* would be available.
(*Galeriscus jacksoni* is not a valid genus or species.)

Races

Bdeogale nigripes (*jacksoni*?)
Bdeogale crassicauda crassicauda (includes *puisa* and *nigrescens*). Dark long-haired. Mainland south-eastern Africa.*
Bdeogale crassicauda tenuis. Small dark, Zanzibar Island.
Bdeogale crassicauda omnivora. Small, light-coloured head and body with relatively short hair. Kenya coastal forests. Might be an ancient relic form near to the ancestral line of *B. nigripes*.

* All members of this genus are subject to considerable variation in the amount of black on the guard hairs and melanic tendencies are discernible both in individuals and in very localized populations (i.e. *nigrescens*).

Above: Dissection of *Bdeogale nigripes*
Below, from top to bottom: Toothrows of *B. c. tenuis*; *B. c. omnivora*, *B. nigripes*



This genus has peculiarly symmetrical toes, relatively long legs and a gait that carries the body well clear of the ground. The molar teeth are expanded, a modification that improves their grinding function and may be related to the primarily insectivorous diet of this genus. Underneath the glossy surface of the guard hairs there is a dense woolly undercoat. Both teeth and fur differ within the genus and show significant racial differentiation within one of the two species.

B. nigripes inhabits part of the tropical forest belt from Mt Kenya to Nigeria while the most widely distributed population of *B. crassicauda*, the nominate race, occupies the woodlands and moist savannas of south-eastern Africa. The isolated Zanzibar Island mongoose, *B. c. tenuis*, which is smaller and darker, may be the most primitive form since the molar teeth show the least expansion. Finally, there is an ecologically isolated population, *B. c. omnivora*, which lives in the Kenya coastal forest. Scarcely larger than *tenuis*, this race, nevertheless, has a more advanced dentition. The greater expansion of the molars, the lighter colouring and shorter length of the fur are features that anticipate their more extreme development in *B. nigripes* and make this population distinctly divergent from *B. c. crassicauda*.

While clearly most closely resembling *B. crassicauda* in size and morphology this is not incompatible with the possibility that *omnivora* might be an isolated relic population deriving from the ancestral stock of *B. nigripes*. How can the peculiar geographic and ecological distribution of the genus be interpreted in the light of this possibility? An early isolation of the Zanzibar population explains the differentiation of *tenuis* from *crassicauda*. Nonetheless, numerous resemblances and the extensive distribution of the latter on the adjacent mainland betray a common origin and suggest that the mosaic of moist savannas, woodlands and forests of south-eastern Africa are an ancient habitat for *Bdeogale*. This makes it very unlikely that the rather distinctive *B. c. omnivora* ever ranged any further south than it does today. In this it resembles some other mammals of the Kenya Coast.

I have already drawn attention to the peculiarity of this region in harbouring forest species that have affinities with populations in equatorial regions far to the west (Vol. I, pp. 75, 149, 199; Vol. II, pp. 44, 684). In two instances colonization of this coastal cul-de-sac from the south would have been virtually impossible because this route was occupied beforehand by a

related but distinctly different form. *Colobus badius rufomitratus* is almost indistinguishable from *C. b. tephrosceles* in western Uganda; yet it differs very greatly from *C. b. kirkii* in Zanzibar and *C. b. gordonorum* from the Uzungwa—Ulanga scarp and valley. Likewise *Rhynchocyon cirnei chrysopygus* is sharply differentiated from *R. c. petersi*, which ranges to its immediate south (and in Zanzibar), while its paedomorphic development implies a closer affinity with spotted forms (which occur further west).

Because the southern approaches are pre-occupied, such distributions suggest that some of the mammals of the Kenya Coast can only be linked with the main forest block across a now defunct equatorial connexion.

The differentiation of *R. c. chrysopygus* demonstrates that genetic isolation of very small populations generally encourages speciation. This trend might be operative for *B. c. omnivora* (perhaps in its small size) but the likelihood of an ancient connexion with the main forest block makes it unnecessary to invoke local isolation with convergence to explain the features *omnivora* shares with *B. nigripes*.

The present locale of *omnivora* may therefore be misleading in that this forest outpost could have preserved one wing of a population that formerly ranged through a much more extensive area (where it has been replaced subsequently by its descendant *B. nigripes*).

If the present distribution of other forest fauna is any guide, the scene of that primary differentiation of ancestral *Bdeogale* might have comprised an enormous belt of forest so that the latitudinal separation now seen along a narrow coastal front might once have occurred between equatorial forests in the centre of Africa and the more open habitats of the south-east.

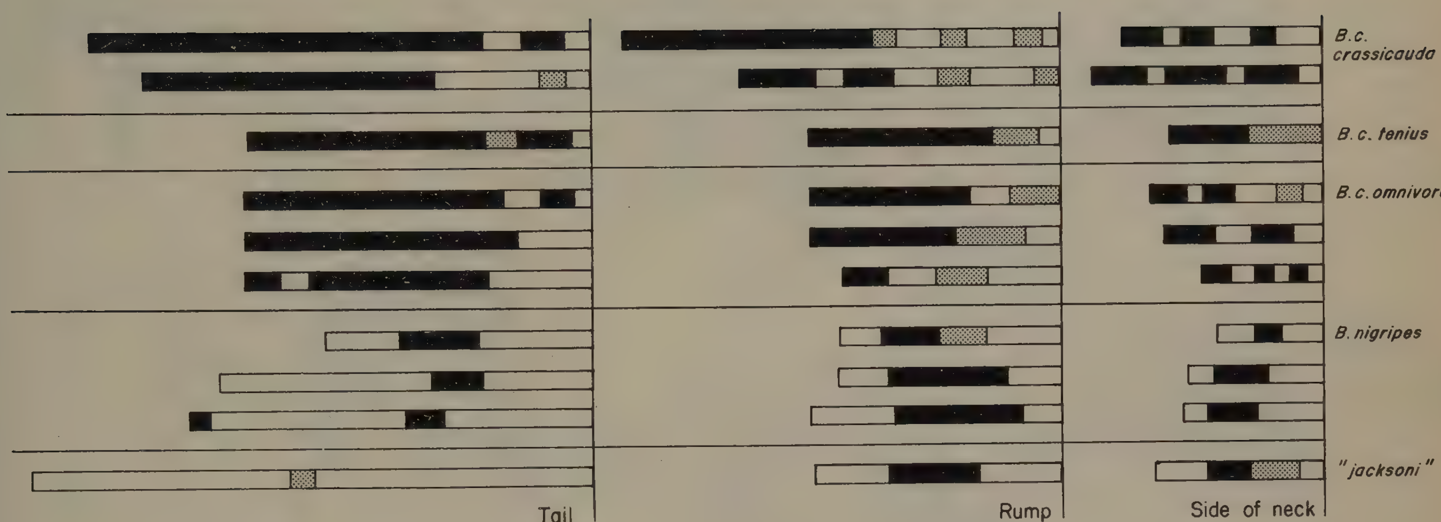
Bdeogale
Hypothetical single population with North-South differentiation

Isolation of populations

Present distribution of species and races

B crassicauda crassicauda
B tenuis
B c omnivora
B nigripes

The special interest of this situation is the adaptation of two closely related forms to forest and savanna respectively. Fire is unlikely to have been an important feature of the environment when this insectivorous mongoose first became a distinct entity. Furthermore, the origins of an ecological divergence



Banding of hairs in *Bdeogale*

in *Bdeogale* are also likely to pre-date the emergence of fire as the dominant factor in savanna ecology. Yet *B. c. crassicauda* is today more of an inhabitant of wooded grasslands that are burnt over every year than of forest, thicket and dense woodland, and the contrast between their grass-dominated environment and the forest floor habitat of *B. nigripes* is extreme. The Kenya coastal strip is a mosaic of forest, woodland, thickets, savanna and cultivation; *B. c. omnivora* probably ranges through all these types of vegetation but is commonest in forest and well developed moist woodland with a closed canopy. *B. c. omnivora* acquired its name because the first specimens contained birds, insects and fruit.

B. c. crassicauda feeds almost entirely on insects, particularly ants and termites; rodents and crabs have also been suggested. Stomachs I have examined contained caterpillars, crickets, grasshoppers, beetles and their larvae, a dragonfly and spiders. Fragments of leaf and stem but no earth implied that they may have been picked off the vegetation.

The black-footed mongoose, *B. nigripes*, also eats insects but this species seems to have a special preference for ants, particularly army ants, *Dorylus* and *Myrmicaria*. Ants are a major feature of the ecology of the forest floor and they themselves harvest the invertebrate fauna of the leaf litter very effectively and their well armed soldiers deter many predators. The biomass of ants must be considerable but trains are constantly on the move and are fairly widely dispersed. If ants are a regular part of their diet, their foraging range should be fairly extensive. Durrell (1954) chased one at the run for nearly an hour before it went to earth in the hollow of a fallen tree trunk,

implying that the animal might have known a fairly wide area. However there is probably a much smaller central area in which the animal lives and here communal dung sites are used, at least during the period adults or families are together. I have had the opportunity to examine dung collected from about 3,300 metres up on the Aberdares. Judging from the sizes of the boluses, of which there were about 40, the site had been used by both adults and smaller animals. About 40% of the adults' diet consisted of insects, principally workers of *Anomma nigricans* (Bolton, personal communication), with various black and green beetles, weevils and caterpillars, there was also a millipede and a small snail, a lizard and a snake's egg but over half the diet was rodents, including at least five *Otomys*, one *Dasymys* and several *Praomys*. Not all the dung included ants but remains of rodents were present in every bolus. The smaller dung had similar contents but in different proportions. About 80% was rodents, at least four *Otomys*, a *Lophuromys*, a *Mus*, a *Praomys* and some peculiar white fur which might have come from a dropped *Colobus* infant. The remainder was mostly lizards and a bird with a few beetles and the odd army ant, which could be interpreted as the young having accompanied an adult while the latter fed on these ferocious insects but

refrained from eating them themselves. The presence of *Dasymus* and *Otomys* suggests that much of their hunting may be conducted in the thick herbaceous growth around swamps. It is interesting that frogs, which are abundant in such habitats, are not represented and that *Otomys* should be the commonest prey for, although a dominant species, the more active murids are also very common yet constitute a smaller proportion of their diet. Beddard (1909) reported remains of a rhinoceros viper in a stomach and Walker (1968) described a *Bdeogale* dying from a swallowed viper fang piercing the gut wall. Collectors of specimens from various parts of Africa have indicated that ants are an important food of *B. nigripes*. It is very likely that the peculiar fur, the short woolly ears and the well-plushed muzzle and feet protect all parts of the mongoose against soldier ants or termites.

When feeding on ants or termites the head may be craned out at a low angle or it may bend down with the mouth vertical. The insects are eaten at leisure and the mongoose frequently lifts its forelegs right up in line with its belly and licks them clean of ants. Likewise, it eventually grooms out many ants from its coat and in this way exploits the swarming defence mechanism of the ants to its own advantage. It should not, however, be supposed that the bulk of its ant supply is lured on to the body.

They also eat carrion and one was trapped on buffalo bones, but it is not known whether it was looking for scraps of meat or associated insects. When offered a live bird, my captive *B. nigripes* ignored it but a dead one was approached and taken into the mouth quite delicately. Although she occasionally made a very quiet growl at me over her food she never worried,

ripped or tore at a bird but, rather, champed the whole mass on the back of the tooth row, crushing bone and tissue slowly but firmly and without effort. Sometimes a paw steadied the carcass. Feeding was nearly always conducted while standing. She gave no signs of sniffing out food and both food and disturbances of any sort were met by an owlish stare and much slow bobbing and peering.

Although remaining very shy long after capture, they are docile and almost completely without expression; Durrell (1954) described one facing a pack of pie dogs as "snarling gently". I never heard my female captive make any other noises than a soft growl and a snort, although a dog-like bark has been reported (Michaelis, 1972).

The animal releases scent from the anal glands when surprised or harassed. The emission of scent is always simultaneous with a fluffing out and display of the tail. It is odd that the forest representatives of this genus

should have somewhat conspicuous colouring while *B. c. crassicauda* is dull brown or black all over. If the colouring of the former in any way parallels that of the zorilla or skunk it must signify an offensiveness that is not perceptible to human senses for the smell, while strong, cannot be called nauseating. However no naturalist has admitted to tasting the animal or its secretions!

Four-toed mongooses are not infrequently seen in pairs, and the animal figured was being attended by three others when it was collected from the trap in the morning. She was a smallish female, possibly still lactating and not yet pregnant again. It was interesting that this animal grew quite substantially in the five months it was captive, even though it had already borne offspring, which suggests that the wide range of adult measurements in this species may be due to a slow and prolonged adult growth.

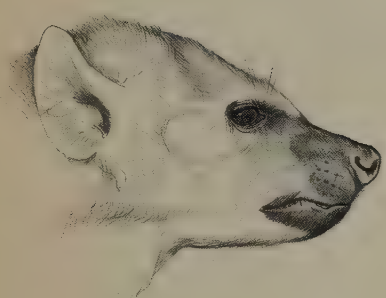
A female *B. c. omnivora* and her quarter-grown young were taken in

December on the Kenya coast and one with a large foetus in the same month. In Liwale, in late November, a female *B. c. crassicauda* disturbed by Ionides in cover made off with a newly born infant held in her mouth which she dropped on being pursued. Nothing is known of their social behaviour.

Michaelis (1972) reports that *Bdeogale* (presumably *crassicauda*) have been implicated as a reservoir for rickettsia. Like civet cats, *Bdeogale crassicauda* are eaten in some localities. They are sometimes encountered dead on highways.

Hyaenas

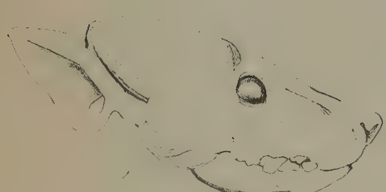
HYAENIDAE **Hyaena**
Crocuta
Proteles



What is a hyaena? Students of mammalian evolution have been dependent on teeth more than any other feature because they are highly diagnostic and because jaws and teeth are more readily preserved as fossils. So great has the dependence been that one commentator has remarked that "it often seems as if the history of mammals consisted of sets of teeth mating and giving rise to other sets of teeth and so evolving more sets of teeth" (MacIntyre, 1966).

Since three of the four hyaenas have enormous specialized teeth and the other tiny pegs, taxonomy has faced an awkward dilemma, made more difficult by an incomplete genealogy of fossil teeth. Many taxonomists would remove the peg-toothed aardwolf, *Proteles*, to another category. Yet its hyaenid affinities are manifested in many details of its anatomy, its behaviour and its chromosomes. At least two students have recognized the diversity of this family and have included *Proteles* amongst the hyaenas. Von Koenigswald (1965), has shown that the two larger genera are not close to one another and have been separated since the Miocene, and Thenius (1966) has gone further and suggested that *Proteles* might be more closely related to *Hyaena* than the latter is to *Crocuta*.

In fact, the disparity of the living genera provides some insight into the evolutionary origins of the family because it removes teeth and the special diets that they imply from the forefront of our consideration.



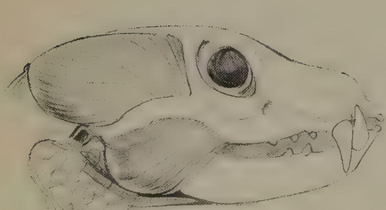
Crocuta

The hyaenas have long been recognized as having emerged from the viverrids at a relatively late stage. The most important phylogenetic change was in the size and proportions of the body.

What then is the significance of a long-legged, long-necked and relatively large-sized terrestrial animal emerging from a short-legged and small-size stock that was probably originally arboreal?

The hyaenids evidently became fairly successful and ten or more extinct species belonging to seven genera are known from African deposits. These include Lycyhyaenas, which were relatively small animals with sectorial teeth (Ewer, 1955a).

Proteles has not yet been found fossil but the other living hyaenas are known from the earliest Pleistocene. The extinct forms are listed opposite (after Savage, in press).



Proteles

The earliest fossils are all from outside Africa and because the viverrids also seem to be of Oriental origin, the primary divergence of hyaenas from the viverrids might have taken place in Eurasia during the early Miocene and Beaumont (1967) has suggested that *Progenetta* from the European Lower Miocene is an early hyaenid. The decline of forest and expansion of open country, which is at the root of our own evolution, provided other

EARLY PLEISTOCENE	PLIOCENE	MIOCENE
Crocuta species		
Hyaena bellax	*Hyaena abriona*	
Hyaena species	*Hyaena* species	*Hyaena* (?) species
Euryboas silbergi	*Euryboas namaquensis*	
Leecyaena forfex	*Hyaenictis preforfex*	
Percrocuta species	*Percrocuta australis*	*Percrocuta algiriensis*
		Percrocuta tobieni
		Ictitherium species

mammals, including the Miocene viverrids, with incentives to colonize new habitats.

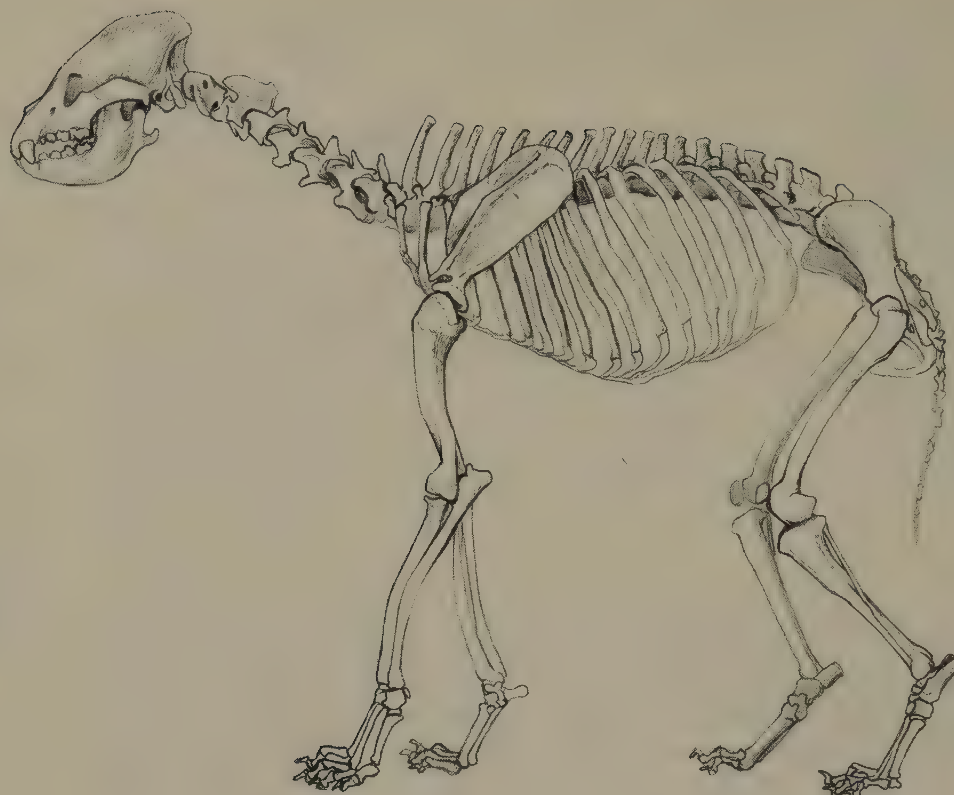
Outside Africa, the canids had seen an earlier and still more diverse radiation in North America and Eurasia. If the living hyaenas are extreme specialists today it is likely that this is because, after an initial expansion into a canid-type niche, the less specialized hyaenas were pushed out through direct competition from the advanced canids that became abundant during the Pleistocene.

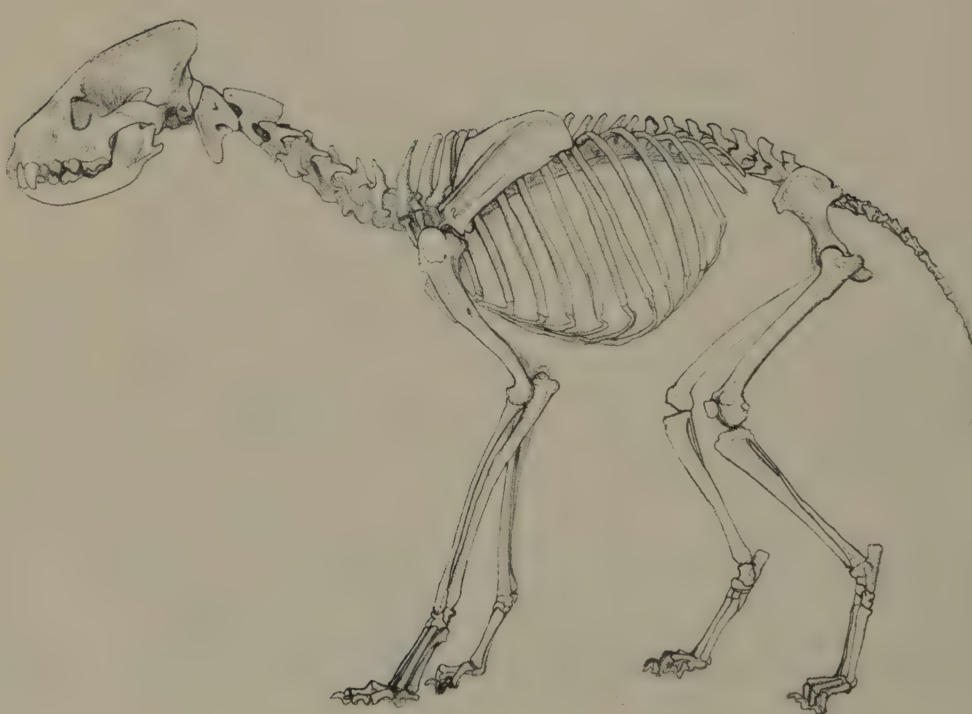
The development of crushing teeth and an ability to extract nourishment from bones was essentially a secondary development, which is not found in all hyaenid lines. The extra advantage that *Crocuta* and *Hyaena* have when they course or forage in direct competition with wild dogs and jackals is that they can consume and digest much that the canids would reject.

That the bone-eating niche was once very much more important than it is today is shown by the independent evolution in America of canids with teeth and jaws adapted for crushing bone, a clear case of convergence with hyaenas. Known as hyaena-dogs, these animals became extinct at the same time as the sabre-tooth and Matthew (1930) suggested that there might have been an ecological association between the two carnivores. Ewer (1973) has made a similar suggestion for the African sabre-tooths and hyaenas. She has pointed out that the sabre-tooths eating habits and the size of the carcass would have encouraged waste for scavengers, the prime candidates of which were hyaenas.

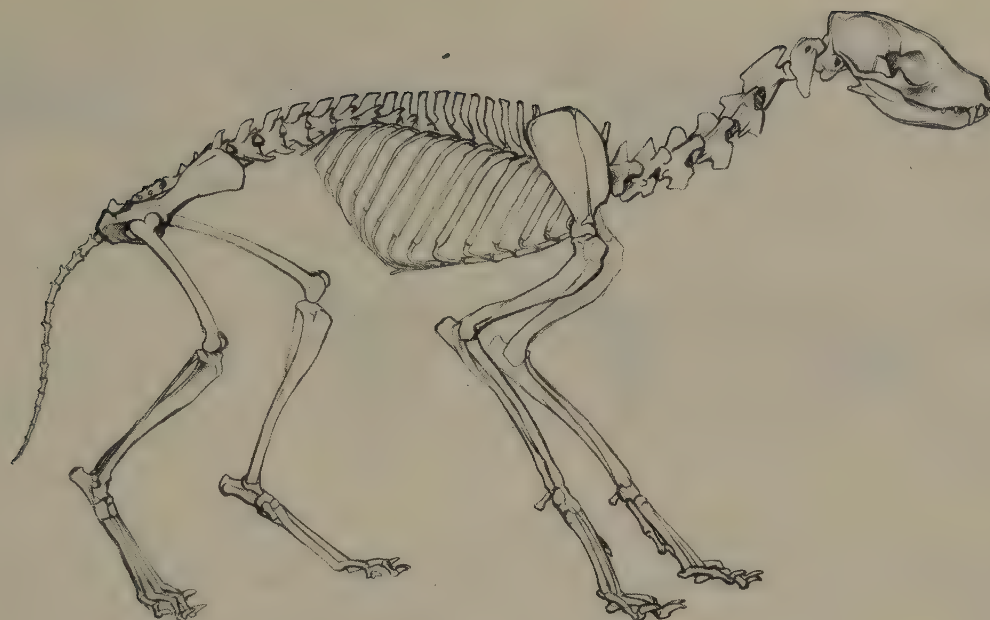
The question of whether extinct hyaenas habitually killed their own prey cannot be extrapolated from the study of living populations. The spotted hyaena is not dependent on lions for its food, even if it consumes their left-overs, but the ability to form packs and kill for itself may be precisely the faculty that distinguishes *Crocuta* from its extinct relatives and had contributed to its survival.

Hyaena is the most prodigious walker and is apparently able to survive on little or no water. It is omnivorous in its diet (see p. 282) and it can subsist on dry bones or scraps and stay fat, even in the Sahara (Osborn, 1968).





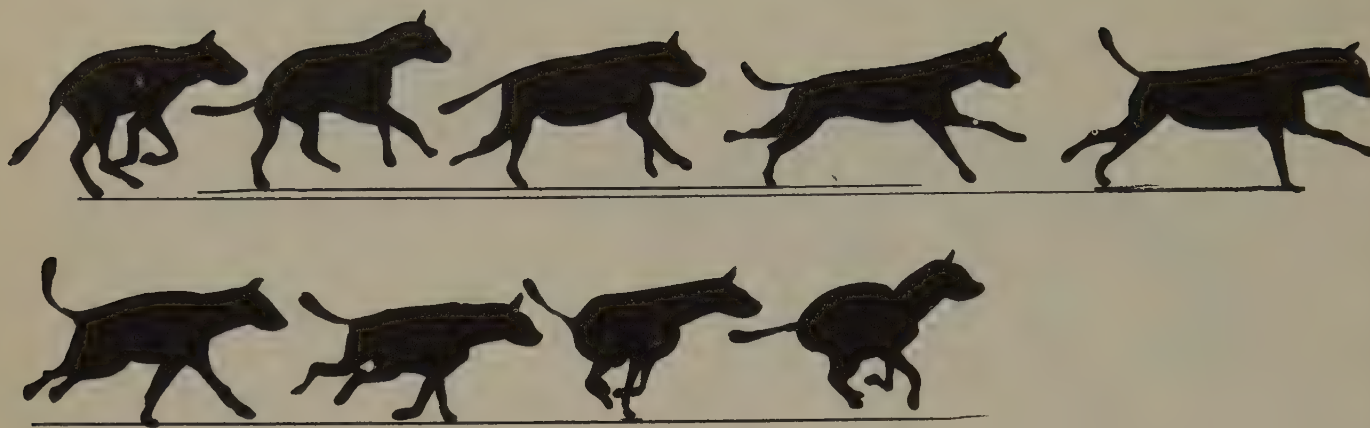
Above: *Crocuta*. Below: *Hyaena*. Opposite: *Proteles*. Note differing proportions of skull and limbs.



The ecological success of the little aardwolf, *Proteles*, has been assured by a virtual monopoly of certain very abundant termite genera in its diet. The adoption of this peculiar but abundant food must have developed after an early divergence amongst the hyaenas. Thenius (1966) suggested that the Pliocene *Ictitherium orbignyi* might be ancestral to *Proteles* but Ewer (1973) considered *Lycyhyaena* the obvious ancestral genus. The aardwolf's chromosomes are similar in number and form to those of the other hyaenas (Ulbrich and Schmitt, 1969) and completely unlike those of the viverrid civet. It has often been suggested that the defenceless *Proteles* is a mimic of the striped hyaena but it is more likely that their resemblance is due to the retention of similar features in both species. Seen in the field, differences in size, colour, gait and general demeanour prohibit any possibility of confusion. Furthermore, the aardwolf scarcely varies at all over its extensive range and there is nothing in its appearance to show that its sympatry with *H. hyaena* in the north and *H. brunnea* in the south has the slightest significance.

Crests are devices for increasing size and are common to many mammals. Striping of the legs may be associated with the ritualized fighting that is common to both species.

Hyaenids often drop on to their wrists to fight and may progress in their burrows in this fashion. Occasionally they feed in this way but for the most part they eat standing. The necessity for a long neck is very obvious at such times and the extension of the neck probably evolved in correlation with the lengthening of the limbs. The aardwolf's proportions can be compared with those of *Hyaena* and *Crocuta* in the drawings of flayed animals and the muscularity of *Crocuta*'s neck and shoulders can be best appreciated when watching



Silhouettes of galloping *Crocuta* (from photographs)

the animals compete to dismember a large beast and carry off limbs or head. The gaits of the hyaenas are influenced by their long necks and the fastest pace of *Crocuta* is not a racing run but a bouncy gallop. Both femur and tibia are long but the lower foot is very short. To avoid extreme flexion on the upper limb during the recovery phase, a galloping *Crocuta* twists its metatarsals in sideways. This device probably reduces the energy involved in contracting muscles (which extend down to the bottom of the tibia), but it might also relate to the inertia of a heavy pad.

The characteristic sloping silhouette of a spotted hyaena is due to the great depth of the shoulder. Very long spinal processes in this region reflect the high bending moments exerted at the shoulder pivot. The strain would be greatest during the gallop and over-extension of neck and hindlimbs might explain why the most exaggerated development of the shoulder occurs in a cursorial species. *Crocuta* also exerts great force while tearing, pulling and carrying heavy weights.

Hyaenid postures are highly distinctive and all species squat with raised tail to paste anal secretions on vegetation. The ritualized postures of fighting in *Hyaena* and appeasement in *Crocuta* are described in the profiles. Unlike a dog, *Crocuta* lifts a hindleg not to urinate but to allow genital inspection.

There are many differences of behaviour and activity between the two genera. Kruuk (1975) recorded *Crocuta* spending only 16% of its time searching for food, whereas *Hyaena* spends 26%. The latter is less vocal than *Crocuta*, which maintains contact through various loud calls. The large overlapping individual ranges and long nightly walks of *Hyaena* suggest frequent contacts with other conspecifics or their traces. This species, like *Crocuta* and *Proteles*, uses its protrusible anal scent glands to mark grass stems, but the scattered distribution of its scent deposits is perhaps influenced by the haphazard nature of its meetings with other hyaenas. The other genera are more territorial and tend to leave their mark on the boundaries of their ranges. In the case of *Proteles*, the territory is always an individual one; in *Crocuta* territories generally belong to a clan (Kruuk, 1975). Kruuk and Sands (1972) have also shown that dung, which tends to be placed on the perimeter of the range in *Crocuta* is deposited by *Proteles* in a small number of latrines which

are not peripheral. The routine of hunting for food can be broken by a visit to the nearest deposit and its location evidently becomes a well-known landmark for the animal. Kruuk's exposure of the social life of *Crocuta* is one of the epics of natural history and his work is reported in the profile of that species.

As they both established their supremacy in the African savannas, man and hyaenas came into intimate contact. During the colonization of northern Europe both man and hyaenas took refuge in caves and thousands of hyaena bones have been found in caves in Kirkdale, Yorkshire, and at Tornewton, Devon. In the context of the peculiar proportions of living *Crocuta* it is interesting that some of its characteristics were even more exaggerated in the race that inhabited the European caves, *C. c. spelaea*, which had especially long humerus and femur and greatly thickened and shortened metacarpals (Kurten, 1958).

Mutual predation has marked man's relations with hyaenas from early times: they were domesticated, fattened and eaten in Egypt, where their boiled genitalia are still believed to cure barrenness. The legends and witchcraft that surround hyaenas in Africa are proverbial.

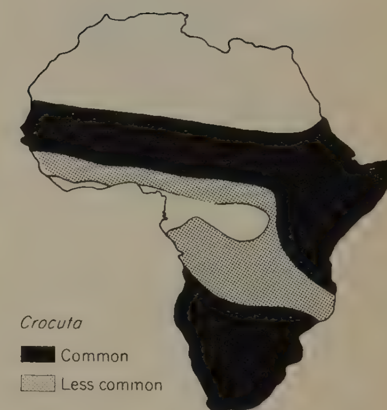
Terracotta hyaena (Nilotic)

Spotted Hyaena (Crocuta crocuta)

Family Hyaenidae
Order Carnivora
Local names
Fisi, Nyangao (Kiswahili), Misi (Kigogo), Fifi (Kisungwa), Empisi (Luganda, Runyoro), Mpiti (Kinyaturu), Lagwara (Lwo), Rara (Lugbara), Mangatiet (Sebei), Ipatama (Kinyiha), Warabes (Kiliangulu), Ebu, Etutui (Karamojong), Ibuin (Ateso) Walaba (Afrendille), Ondilili, Oln'gojine (Masai), Makatiet nyenegea (Elkoni), Kimatet (Kalenjin), Otoyo (Luo), Ebowu (Madi), Ibau (Kipare, Kizigua), Mbitingaau (Kimeru), Mbiti (Kisukuma, Kikamba, Kimaragoli), Hiti (Kikuyu), Mbichi (Kirangi), Mbisi (Kitaita), Namunyu (Luhya), Ingurunju, Ifulu (Kichagga), Imembe (Jita).

Measurements
head and body
95—150 cm
(on average females
12 cm longer than males)
height
70—91·5 cm
tail
30—36 cm
weight
40—86 kg
(on average females
6·6 kg heavier than males)

Spotted Hyaena (Crocuta crocuta)



The spotted hyaena has powerful forelegs and shoulders, a long neck and heavily built skull and teeth. Its round ears and spotted coat are distinctive. Various races have been described but, while there are regional variations in the size of hyaenas, colouring and markings are subject to considerable individual and age difference. The general trend is from dark well-marked spots in the young to pale almost spotless bodies in the oldest animals.

Fossils from Eurasia have included races that are both substantially smaller and larger than the living species.

The most widely publicized peculiarity of the spotted hyaena's anatomy is the resemblance of the female's with the male's genital organs. Females are therefore almost impossible to tell apart from males in the field (except for their rather larger size). Hyaenas were therefore once reputed to be hermaphrodites. The female clitoris mimics the male penis to a quite extraordinary degree. Like the penis it is capable of considerable elongation and turgescence and is protected by a foreskin. It is likewise perforated by the urogenital canal and in young females the opening scarcely differs at all from that of the male, although with sexual maturity it elongates and thus allows an adequate opening for copulation. In addition to the peniform clitoris, the female has paired swellings in the position of the male scrotum which consist of physiologically non-functional fibrous tissue.

Furthermore, the genitalia in both sexes develop at a very early age, soon reach adult size and are capable of erection at the age of a few months, appearing quite grotesquely disproportionate on the little animal displaying its turgescent genitalia with one leg raised. Genital display is particularly common in youngsters and has nothing to do with sexual behaviour but is extremely important socially, functioning as an appeasement gesture by inferior classes of hyaena towards their superiors and by the male towards the dominant female. Kruuk (1972b) has suggested that the female's larger size and dominant status may have evolved in the first place to deter male cannibalism of the young and it is possible that this reversal of sexual dominance has led to an inversion of the sort of mimicry found in several primate species (see Vol. I, pp. 159, 215 and Wickler, 1964, 1965), where mimicry of the female characteristics is accompanied by "presenting" gestures.

From very early times observers have remarked that a curious mixture of aggressiveness and timidity is typical of *Crocuta* behaviour, not only in its relations with humans but within hyaena society itself. Terrible wounds can be inflicted very easily and a capacity for attacking or chewing up any available animal matter has both ensured the hyaena's status as Africa's commonest large carnivore and also made it imperative that in the frequent meetings of a semi-solitary, semi-social predator some sort of damper should be put on aggression. Demonstrated inferiority tends to dispel tension and it seems that the display of male characteristics in *Crocuta* serves this purpose. It also makes those hyaenas that have managed to come into close contact more

interested in another's hind end rather than the dangerous front end.

Originally distributed from end to end of Eurasia, *Crocuta* was a dominant carnivore throughout the second half of the Pleistocene and Kurten (1968) correlates the appearance of a dwarf form in Post-Glacial Europe with the development of agriculture. The reasons for its extinction outside Africa are not at all clear.

Until very recently the spotted hyaena has been a common and widespread species over a great part of sub-Saharan Africa, but it has suffered a decline all over the continent in this century. In many areas of East Africa the local inhabitants regard them as such a familiar part of the scene that little action is taken against them and they were even protected in some localities, but officials originating from other areas and countries have generally encouraged widespread extermination by means of poisoning, to which hyaenas are particularly vulnerable. In Kenya the veterinary department is currently poisoning hyaenas on a large scale.

Their present distribution, therefore, bears little relationship to their original range, which was practically all the more open habitats. They were particularly common in dry acacia bush, open plains and rocky country where there was abundant wildlife. They seem to have been less common in heavily wooded country and are generally absent in true forest, although they may follow tracks or roads deep into forest areas. They often live at high altitudes and have been recorded as high as 4,000 metres in Ethiopia and East Africa.

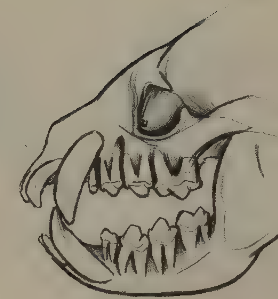
Their distribution is determined primarily by the availability of prey and the largest numbers of hyaenas are to be found in the areas where there are ungulate concentrations. Here they tend to live mainly off three or four dominant species. Where food resources are more dispersed hyaenas tend to forage alone and the size of the prey they can tackle is reduced accordingly.

In spite of its widespread reputation as a formidable stock killer and in spite of not infrequent sightings of *Crocuta* packs killing large wild ungulates, the traditional image of the hyaena as a scavenger has only been dispelled by Kruuk's intensive studies on the Serengeti (where as early as 1936 "hordes of hyaenas" were described killing gnus and gazelles). In his 1972 monograph, "The Spotted Hyaena", Kruuk has explored the Serengeti hyaenas' behaviour and ecology as an interrelated whole and his study is one of the finest written on any African mammal and is the source of most of the information on this species.

Crocuta is probably the most numerous of all the large predators and there are many more hyaenas than lions or cheetahs or wild dogs. Furthermore, the spotted hyaena is an adaptable and opportunistic hunter and scavenger with several advantages over all other larger carnivores.

First of all is the capacity to eat and digest skin, bone and other animal waste. In this way it can gain nutriment from every part of its kill and can find a plentiful food supply left by all types of carnivores and by man, both in the form of leftover bones and offal and in the faeces of large cats, wild dogs and man. *Crocuta*, in functional terms makes the most efficient use of animal matter of all African carnivores, because in addition to consuming every part of its own prey it extracts organic matter from the waste of other predators. The consumption of the entire carcass is combined with other

characteristics that give *Crocuta* an edge over its competitors. It bolts its food at great speed and as soon as it is possible a carcass is dismembered and individual hyaenas or small groups scatter widely with the pieces. Kruuk has described 38 *Crocuta* entirely demolishing a zebra mare in fifteen minutes and a young zebra was dismembered in seven minutes. This total destruction leaves very little evidence of the hyaenas' nocturnal activity the following day, hence the general underestimation, even by experienced naturalists, of the spotted hyaena's role in the large mammal communities of Africa.



Hooves, hair and horn are not digested and while much hair passes through the gut a lot tends to be regurgitated in pellets near the den or diurnal resting spot. Dismembered prey is generally eaten not very far from the site of the kill, but in some areas hyaenas sometimes carry pieces back to the den, where bits of bone may lie around or even accumulate in the dens.

Wherever animal waste is available, whether through the selective feeding of other carnivores, through the activities of human villagers and pastoralists or through the vicissitudes of nature—disease, famine, accident—hyaenas left to themselves can be expected to absorb most if not all of this waste. *Crocuta* is a scavenger in direct relation to the amount of waste there is about, subject to there being no easier yet more attractive alternative. Thus fresh bones and carrion may be left while there is a glut of vulnerable calves during the short birth season of certain plains ungulates.

Crocuta is superior to the striped hyaena and also to leopards, cheetahs and wild dogs in the plasticity of its behaviour; for, like the solitary species, it can forage singly on scattered small prey and carrion or, like the social species, it can live and hunt in a group to exploit concentrations of larger prey. Unlike the lion, which tends to kill a random sample of the larger ungulates, the hyaena eats the weak, the diseased, the injured and the dead of almost any mammal, bird, fish or reptile irrespective of its size or species. Thus hyaenas have been seen to kill a very old sickly black rhino (Deane, 1962), adult buffaloes and lions (Pienaar, 1969) and fish in shallows. They are, of course, well adapted to tackle tortoises and pangolins.

The numbers of sick or injured prey animals fluctuate widely in nature, whereas the numbers of hyaenas have not been observed to change accordingly. When conditions are at their most favourable for the prey species, hyaenas are still consuming as much as they were when the prey were more vulnerable. Nonetheless, the hyaenas still tend to pick out weaker individuals.

Kruuk's comparisons between *Crocuta* populations in Serengeti and in Ngorongoro revealed significant differences. On Serengeti both hyaenas and their prey live at much lower densities as they are forced to move with the seasons and so use a much more extensive area. By contrast, conditions are almost optimal for both the predator and prey populations confined within the crater. In both areas there is a close correspondence between the relative abundance of the prey species and their presence in the hyaena's diet but differences in the make-up of their kills reflect the availability of prey to hyaenas and in Ngorongoro there is good evidence that *Crocuta* is the major controlling factor in the population dynamics of the resident gnu, *Connochaetes*.

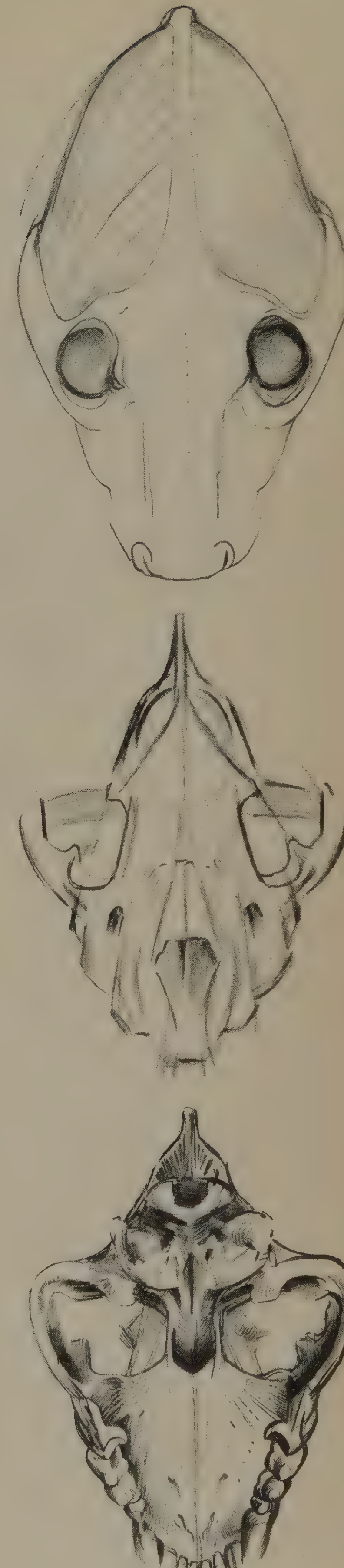
In Serengeti, hyaenas, like other predators, become very dependent on the gazelles while the gnu are at the extremities of their migratory range. Kruuk estimated that gazelles constituted nearly one-third of the prey animals, the gnu accounted for just over one-third, while 20% were zebras. Zebras formed a similar proportion of their diet in the crater, but gnu made up two-thirds and gazelles only 7·3%. Nearly two-thirds of the Ngorongoro gnu were killed before the age of one year. A more balanced ratio of age

groups was apparent in the Serengeti kills and it is evident that hyaenas significantly alter the age structure of gnu in Ngorongoro (see gnu profile).

The correspondence between the relative abundance of prey species and their appearance in *Crocuta* kills is well illustrated in the records published by Pienaar (1969) for the Kruger Park. If these records truly reflect the ratios of hyaena kills, zebras seem inexplicably to come off more lightly than they do in East Africa. Pienaar thinks the kudu and waterbuck cows render themselves particularly vulnerable to both hyaenas and wild dogs by their attachment to a locality.

Kruger National Park (data from Pienaar, 1969).

Species	No. of *Crocuta* kills. Total 172	Approx. percentage of total	Estimated percentage of relative abundance in park
Impala	104	60·5	53·41
Gnu	20	11·5	7·76
Buffalo	2	1	8·70
Zebra	1	0·5	8·07
Kudu	17	10	2·88
Waterbuck	19	11	1·75



The capacity of *Crocuta* to take advantage of very local concentrations of vulnerable prey was noticed on the Mweya peninsula (Lake Edward) during the 1950s before both hyaena and hippo populations were artificially controlled. A pack of hyaenas was then thought to be subsisting very largely on the numerous hippopotamus calves born along this stretch of shore. At the south end of the same lake, remains of hippopotamus have been found in the stomachs of hyaenas but here topi and Uganda kob are the two dominant species supporting a flourishing hyaena population. In Aswa Lolim, in western Acholi, hyaenas live mainly off Uganda kob, Jackson's hartebeest and perhaps oribi. In Tarangire, on the edge of the Masai plains, the hyaenas follow the zebra and the gnu migrations and it is probable that somewhat the same situation occurs there as in Serengeti.

Kruuk (1972) observed packs with distinct prey preferences and he noticed short-term preferences, which he suggests may signify a tendency to vary the diet. Zebra-hunting hyaena packs were recognized as such by Kruuk long before they selected a quarry. Up to 25 hyaenas will pursue a family of zebras and, evading the rearguard attacks of the stallion, will attempt to isolate an individual animal from the tightly bunched family. If this object is achieved all the hyaenas converge on the zebra and tear it apart. The victim is most frequently a mare or a youngster. Stallions or mares will sometimes drive off or even kill hyaenas in defence of their young, and the misdirection of a hyaena's instinct to disembowel its prey is illustrated in the following report:

> "A hyaena was trying to take a very young zebra foal on the floor of the Ngorongoro crater. The zebra mother made several rushes at the hyaena, during one of which its forefoot struck the hyaena's belly causing a wound from which the

> entrails protruded. The hyaena then proceeded to draw out and devour its own entrails and so perished" (T.P.R., 1957).

Hyaenas do not generally attack larger prey on their own but each hyaena acts on its own and the following report, while illustrating the general pattern of hyaena kills also shows that single hyaenas can kill animals larger than themselves:

> "the hyaena closed on a running adult wildebeest and bit him in the flank, opening the stomach cavity. The hyaena was swallowing entrails as both animals were running. Finally the wildebeest dropped and the hyaena carried on eating his victim alive" (T.P.R., 1960).

When the body wall has been torn open, hyaenas eat the testicles, udder and viscera (sometimes deliberately leaving the lungs aside). The large muscles of the upper legs are quickly consumed and the limbs are torn off and carried away by individual hyaenas. Animals finding themselves with a horned head tend to start with the muzzle and end at the horns.

Sometimes hyaenas try to cache parts of carcasses under water and a hyaena dropping meat and bones in a pool has been observed to try and push the lungs under water with the greatest persistence. Kruuk (1972b) observed hyaenas diving for bites out of a drowned gnu and only coming to the surface to swallow, then disappearing beneath the surface again. As well as appearing to enjoy water as a cool playground hyaenas succeed in catching catfish, *Clarias*. Stephenson-Hamilton (1954) watched a hyaena standing in shallow water with forelegs well straddled out and in this position snapping up any fishes large or small that came within reach.

Although they need to drink, they are able to do with very little water and that very seldom. Kruuk reports even a lactating female going without water for over a week. Intervals of five days between meals have been recorded but their food consumption at one sitting can be as much as 14·5 kg, a meal for which their capacious stomach is well adapted. Kruuk worked out an average actual consumption of 1·5—1·8 kg per hyaena per day. The killing rate, which includes waste, was estimated at 2 kg in the crater and 3 kg in Serengeti.

Occasionally hyaenas, like lions, leopards and other carnivores react to a superabundance of prey by indiscriminate killing. Watson (1950) reported hyaenas scattering and killing sheep that had been penned in a mud and wattle hut at Serere stock farm. One or two were eaten but the rest only had the tops of their heads bitten or were disembowelled. After a dark and stormy night on the Serengeti plains Kruuk found 109 gazelle dead or injured by hyaenas only a few of which had been partly eaten.

Kills can attract very large numbers and over 50 hyaenas have been seen feeding together. The females are dominant but there is very little outright fighting in spite of much noise. Each individual tries to eat faster and thus get more than its neighbour, and as soon as limbs or pieces can be torn off or carried away the concentration starts to disperse. A hyaena carrying away a piece of the kill will sometimes be chased by another; if this is in earnest, speed of flight or social dominance soon settles the outcome. If the hyaenas are already well fed a playful circular chase with tails in the air may take place. Chasing and bone-carrying are common forms of play in both the young

and adults and Scott (1959) watched a party of ten hyaenas romping in water in Uganda.

A very typical feature of the hyaena's social behaviour is bouts of intense interest in a scent mark, this "social sniffing" is associated with a group reinforcing its territorial boundaries.

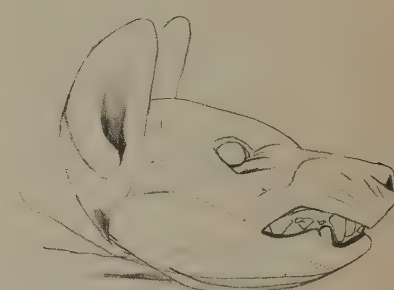
Like the striped hyaena, *Crocuta* marks grasses with the anal gland, which is brought into play by eversion of the rectum around a grass stalk that has been dragged between the squatting hindlegs, but unlike *Hyaena*, *Crocuta* tends to mark in parties and marking is associated with penial/clitoral erections. Kruuk found it most commonly performed by a group patrolling their territorial boundary. It was also observed when lions were about, around a kill after feeding, by males and cubs near dens and by the sight of strange hyaenas. Aggressive implications are suggested by an association of the anal bulge with expressions of aggression, whether against strange hyaenas or lions. Another aggressive use of scent was discovered by Kruuk when he observed hyaenas scraping or pawing, an action that deposits scent from small glands situated between the toes. (The male also performs this action when courting a female.) Dung is also used as a territorial marker in latrines that are particularly common along the boundaries, dunging is often accompanied by anal and interdigital scent marking.

Excreta are seldom found in the immediate vicinity or down the hyaena's dens, although there is usually a very strong smell of urine. Dens vary greatly in size and in my experience are most commonly disused *Orycteropus* holes, which may be extended by the hyaenas. The choice by *Orycteropus* of

raised, dry ground for digging holes in the wet season may be the reason why the dens are so often found on ridges or minor watersheds.

Very large numbers of hyaenas are sometimes gathered at a den, and a well-known site near Kajiado sometimes accommodated over 80 hyaenas (Croydon, personal communication). At this site the hyaenas made use of natural cavities along a rocky cliff, around which the bare soil was compacted over an extensive area by the passage of their feet, the site having been tenanted for as long as could be remembered by the local Masai. It was, however, very readily and completely evacuated for a while after live traps had caught a few animals, only to be gradually recolonized some months after the disturbance. At this den huge numbers of fleas covered any visitor in a matter of seconds. Temporary dens, often small holes dug by *Orycteropus*, seldom accommodate more than a female with her young or a single hyaena.

Genital greetings are frequently seen around the den, as any returning animal will either greet or be greeted in this way, and it is usually initiated with a moaning noise by the younger or smaller animal. Sometimes the inferior animal may even fall over in apparent servility as it raises its leg ever higher, meanwhile whining softly. This ceremony clearly assists known hyaenas to re-establish contact and appease aggression. Kruuk observed one female from a group of mothers on a den retrieve a wandering cub. Another female growled and snapped at her, whereupon she immediately presented her genitalia. Such exposure could be dangerous and Kruuk did see one hyaena with a mutilated penis, but aggressive intentions are generally revealed before such exposure. Kruuk has described the meeting of two strangers with an established group.



> "When the two came close all eight got up and sniffed the new hyaenas briefly along their sides and heads; their tails and manes rose as they did so and suddenly one of the eight snapped at one of the new ones. The latter jumped away with a yell",

whereupon the strangers were chased away. That the genital display serves to restrict aggression in dangerous situations is suggested by the fact that it has been observed between hyaenas after hunting, sometimes immediately after the kill and sometimes after an abortive chase.

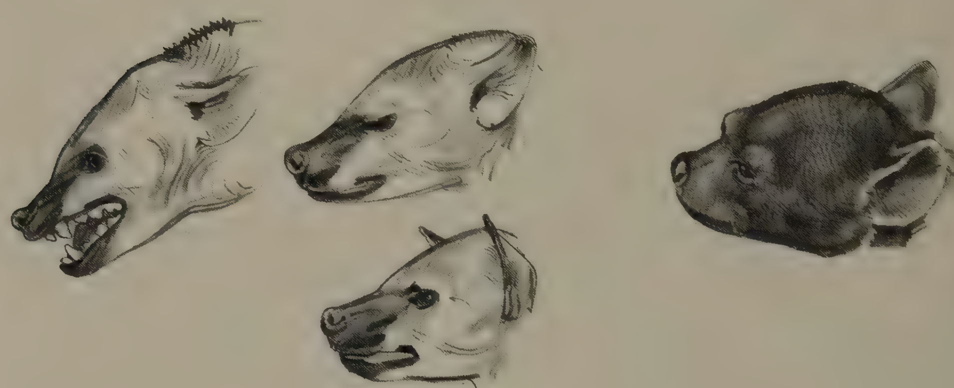
Although a party of hyaenas may sometimes be led by a large female or females and the smaller animals tend to take up the rear, this expression of the females' general dominance over males disappears during activities such as hunting, patrolling and marking territorial boundaries and during aggressive encounters with other hyaena groups or lions.

Hyaenas have occasion to bait lions most frequently when the cats have appropriated their kill or when the hyaenas are attracted in numbers to the lions' kill. Baiting may consist of a frustrated hunting or attacking impulse tempered by fear. On the other hand, it has similarities with bird mobbing. As Kruuk suggests:

> "it may well be that by mobbing predators are induced to leave the area and since it is to the hyaenas' advantage to have the competitive and dangerous lions out of the way there may be similarities between the hyaenas' behaviour and that of the mobbing birds."

However, there is a resemblance between lion mobbing and what Kruuk calls "female baiting" when several males gang up on a single female and threaten her with calls and gestures very similar to those displayed at an outnumbered lion. The female is seldom hurt, but this behaviour illustrates the typical hyaena pattern of alternating individual timidity and group aggression, for although a male on his own would be dominated by a female, the roles are reversed in this situation and it is the female that cringes and yells when baited.

It is possible that a female monopolizing a kill or some such situation



may occasionally trigger (but only in males) an "anticompetitor response" that would normally be directed at lions or strangers. Likewise, the young may need the genital display to help switch off or divert the adults' predatory impulses. Since adults readily kill the young, elaborate built-in mechanisms are required to separate the individual's predatory and social impulses and avoid dangerous actions being discharged at the wrong object.

Hyaenas have keen senses. They can see, smell and hear well and will often circle other hyaenas or human camp sites, apparently to get down wind and sniff. Their pace can be surprisingly fast and they have considerable endurance when coursing antelopes. The spoor is highly distinctive, the forefeet making broad round impressions and the hindlegs smaller and more elongated ones. The dung, white and chalky from the breakdown of bones, is also distinctive and highly visible.

The activity of hyaenas varies very greatly with the environment and the seasons and also with the distribution of their prey. Kruuk found that 80% of a hyaena's life is spent lying down and he also found peak activities between 5 p.m. and 1.30 a.m. and from 5 a.m. to 8 a.m. Hyaenas generally rest between 10 a.m. and 5 p.m. except in cool overcast weather. They prefer damp cool places and may sometimes be seen wallowing in shallow pools.

Eloff (1964) recorded hyaenas in the Kalahari walking as much as 80 km in a night. Hyaenas following migratory prey from their dens on the plains in Serengeti might sometimes cover a distance approaching this, and prey is sometimes so dispersed that mothers leave their young for several days.

The social structure of hyaena populations is extremely flexible and is adapted to the opportunities offered by the environment. Over a great part

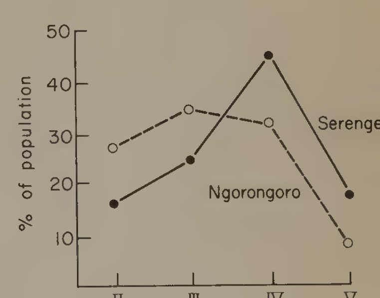
of their range they tend to be seen as solitary animals or in pairs, but where the available prey population can feed a higher density of hyaenas, the advantages of social living and hunting seem to bring hyaenas together, sometimes temporarily, or, in areas with a resident prey population, permanently. In parts of central Tanzania and north-eastern Uganda, hyaenas which fed to a large extent on the debris of the scattered but fairly dense human settlement, have been observed to come together in packs periodically, at which time they can become a danger to both stock and humans. Whether the increase in the hyaena population has been responsible or whether they were brought together by a local resource such as rubbish tips or impala herds or whether socializing was spontaneous has never been determined, but reports of hyaenas suddenly becoming dangerous in packs have not been uncommon in Game Department records.

In his comparisons between Serengeti and Ngorongoro, Kruuk found that hyaenas walking about on their own or in twos are twice as common in Serengeti, where the overall density of both hyaenas (0·12 per sq km) and their prey is much lower. In the crater, with 1·5 adults per sq km, conditions seem nearly optimal and there are recognizable units of up to 80 hyaenas, which Kruuk has termed "clans", which share, patrol and defend a hunting territory against other clans. The fact that the hunting territory must support its hyaenas ensures that there is a close correlation between its size, the available prey and the number of hyaenas in it. As the numbers of predator and prey must be subject to some fluctuations, boundaries may also be expected to be altered and Kruuk did indeed observe changes in the size of territories which could be correlated with the number of hyaenas in the clans, one of which grew from fifteen to thirty-five members in two years. Sex ratios were found to be equal in Ngorongoro. A lower count (36%) of females on Serengeti kills might well indicate that a lower density led to less pressure on the mothers to get to the kills.

Differences in population structure were observed by Kruuk who estimated a 13·5% annual recruitment in the crater and perhaps 5% in Serengeti, where there is a high cub mortality, probably because of the distances travelled by foraging mothers away from the den. In Ngorongoro the main loss from the population is of yearlings; 30% of Kruuk's marked sample disappeared within three months of being independent. A third of all the Ngorongoro females had cubs and were lactating at a time and their average birth intervals were 17·4, (9—26) months. Judging from disappearances of marked individuals, Kruuk computed a mortality rate of 16·7% per annum.

Crocuta show no evidence of being individually territorial, instead they form bonds very easily and dissolve them equally readily; but the formation of groups seems to be accompanied by built-in social behaviour that results in the emergence of *group territories*.

This association does not affect the capacity of an individual hyaena to live a solitary or social existence at any time. The benefits that the collectively-held territory confers are probably greatest for the young in that they are likely to be born in a den where protection from strange male hyaenas and other predators is more effective and they may have a better chance of food where the numbers feeding at a kill are restricted. As many prey species can fend off one or two hyaenas but cannot protect themselves so effectively



Percentages of age-classes in two Tanzania populations (after Kruuk 1970)

Clan ranges in Ngoro ngoro crater

= Clan dens

▲ = latrines used by Mungi and Scratching Rocks clans (after Kruuk 1972)

from a pack, this fundamental advantage is shared by all members in the form of larger carcasses available more frequently. Kruuk was able to define the boundaries of the Ngorongoro clans, sometimes with considerable precision, and was therefore able to confirm that prey was seldom pursued far outside the territory and, if a kill was made inside another territory, it was generally lost to the owners of the land. He described one spectacular boundary confrontation in the Ngorongoro crater: a kill had been made in an area between two groups that Kruuk had named the Mungi and the Scratching Rocks clans, as the hyaenas converged Kruuk

> "had a beautiful panoramic view of how the others were following, coming in from all over the Scratching Rock's range. Finally there were twenty-six of them facing seventeen hyaenas from the Mungi range. The Mungi hyaenas first continued feeding, but when the tightly packed contenders slowly approached in aggressive attitudes, uttering low calls and fast whoops, the Mungi hyaenas withdrew to the other side of the carcass. . . . For a brief while there was a great turmoil of 43 hyaenas chasing each other. Within seconds the Mungi animals fled and the Scratching Rocks hyaenas ate. But their victory was very short-lived; after they had eaten for about one-and-a-half minutes the Mungi pack was back again and the roles were reversed. Again a wild turmoil and chase followed, this time leaving the Mungi hyaenas eating. In this way, the carcass changed owners 12 times in 25 minutes; once the two opposing packs were even pulling at it from opposite ends at the same time."

Once the carcass had been dismembered and eaten the hyaenas dispersed and drifted back to their home ranges. Although both sexes participate equally in the defence of territories, males have less attachment to the clan than do the females and one male, notable for his initiative in killing large prey, belonged to two clans. Another male changed clans but took a year to be fully accepted in the new area.

It is possible that the "social sniffing" mentioned earlier is an important mechanism in drawing hyaenas together for the purpose of boundary marking, as this commonly observed behaviour often precedes a group's embarkation on a "patrol", during which time the hyaenas smear grasses together (anal marking), paw the ground (interdigital marking) and defaecate (faecal marking). See map of faecal markers opposite.

Kruuk thought these groups gave the impression of patrolling for the sole purpose of "social sniffing", marking and meeting neighbours. He also described a hunting group stopping at a faecal marking or "latrine" on their clan boundary, spending several minutes scent marking, scratching and defaecating and staring into their neighbours' territory before returning.

Kruuk also noted a visible change in the demeanour of many hyaenas as they leave their own territory. In an excellent illustration of how the fiercest aggression may be redirected or even reserved for intraspecific trespassers, he described how nine hyaenas sat quietly watching three lions feeding on their own stolen kill. A strange hyaena coming on the scene was attacked instantly and with great ferocity.

I once herded a single hyaena for some kilometres with a vehicle until it came within sight of a group of five strange hyaenas that immediately charged it. From this point the hyaenas were so preoccupied with the chase that ensued that they all ignored the vehicle entirely.

The impulse to come together and defend an area does not depend on long-standing residence, however. The Serengeti hyaenas, following the migration of the gnu and other animals, form temporary clans which defend land. Nonetheless, there is evidence that in spite of the seasonal movements and considerable mixing up of the population, individuals tend to return to the localities they know well.

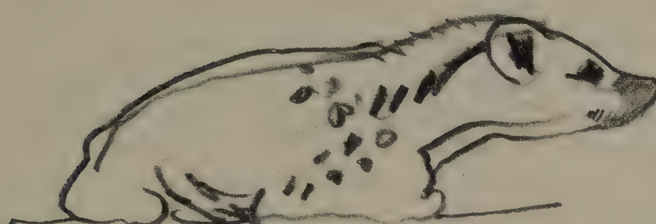
The hyaenas' strong preference for open country is exemplified by their retention of bases on the nearly empty plains during the dry season. From large communal dens, in which the females and their cubs congregate, the adults follow prey along well-known tracks to the dry-season ungulate concentration areas 25 km, or more, away from the plains margins. Kruuk found 72% of the known hyaena dens within a belt 5 km wide. On the other hand, during the rains the hyaenas live in numerous small dens scattered over the plains, which allow hyaenas to converge from many different areas and live among their prey grazing on the plains.

While such movements must primarily be determined by the need to follow prey, it is possible that yearlings may initiate movements away from established dens as they explore further afield. The only record of a marked hyaena leaving the Ngorongoro crater population was of a yearling that was subsequently seen near Olduvai, 20 km away from its home range. Disturbance such as the Kajiado incident mentioned earlier may also lead to the decamping of entire groups.

The movement of adults over long distances, with the risk of starvation or accident that it entails for the cubs, constitutes a major limitation on the Serengeti hyaenas. An important factor in this sort of movement seems to be the hyaenas' "reluctance" to live in woodland. In true miombo woodland, the tse-tse flies favourite habitat, the hyaenas appear to be relatively scarcer than elsewhere and Harrison (in Swynnerton, 1936) noticed hyaenas snapping and tail-lashing when attacked by tse-tse flies. As nocturnal animals, one could expect hyaenas to escape the worst of tse-tse flies' attentions but Swynnerton (1936) reported trypanosomes in hyaenas and it is possible that tse-tses are in some unknown way a controlling factor on hyaenas. In this connexion it is worth mentioning a sudden decline at the end of 1954 in the once-numerous hyaenas of what is now Kidepo National Park. This coincided with the cutting of a tse-tse control line to the south of this area. This unusual example of a natural population crash in hyaenas would have been very interesting to investigate. Particularly intriguing are the possible implications of a subtle ecological disturbance following tse-tse control clearing of vegetation in the vicinity. Baker (1968) has suggested that the trypanosomes found in the hyaena blood are acquired through eating infected animals rather than directly through the tse-tse fly bites.

Sachs *et al.* (1968) found antibodies for rinderpest, brucellosis and anaplasmosis in Serengeti hyaenas. Pienaar (1969) remarks that hyaenas feeding on large numbers of anthrax carcasses during the Kruger Park 1960—61 epizootics, failed to contract it and he thought hyaenas became a factor in preventing the spread of both anthrax and foot and mouth; he also records the intramuscular nematode *Trichinella spiralis*, which can cause emaciation and paralysis in the host. Dinnick and Sachs (1969) describe a tapeworm, *Taenia longojinei*, that has its larval stage in the sacrum of large ungulates, where only the hyaena can release it to complete its cycle in the hyaena. Another tapeworm living in the hyaena's gut is *Taenia hyaenae*, the larvae of which are encysted in the muscles of ungulates. Both parasites are normally well tolerated.

The two most important animals influencing and limiting hyaenas are man and lions, both of which provide large quantities of waste but also



compete for the same resources. Obviously the number of competitors and the amount of food available will influence the relationship. Kruuk showed that at Ngorongoro the reduced lion population was benefitting from the very dense hyaena population and arrived at 51 out of 244 observed hyaena kills, reversing the traditional image of killer and scavenger. However, there are few areas where lions are commoner than spotted hyaenas. It is also very rare to see these cats and *Crocuta* feeding together from the same carcass and lions quite frequently kill hyaenas.

Wild dogs provide hyaenas with waste in the form of bones and faeces and while freshly killed carcasses may occasionally change hands in either direction the wild dogs are generally dominant, which, as Kruuk points out, is probably because of their concerted assistance to one another while the hyaenas, although in groups, are operating each one for itself.

Other carnivores provide waste and hyaenas have been known to steal prey directly from leopards, cheetahs, jackals and baboons. Warthogs sometimes share dens with hyaenas and may be tolerated better than the males of their own species but Deane (1962) suggests that cubs may sometimes be killed by the adult pigs.

Of twenty-four records of hyaena deaths, Moss (1976) records thirteen killed by lions, four by other hyaenas, two by man and the remaining five died through disease or starvation. Fighting amongst hyaenas can occasionally lead to fatalities and the young ones face real danger particularly from

strange males but the main expression of intraspecific competition is over food and the rapid consumption of kills would tend to favour the fittest animals. This factor may explain the "younger" population Kruuk found in Ngorongoro (see chart). Crocodiles are a danger to hyaenas which they seem to recognize, using water as they do to cache food and play in. Kruuk records them leaving a zebra to rot in a crocodile-occupied pool.

Crocuta is polyoestrous with a two week cycle. A female in season often attracts a noisy crowd of males, the squabbling calls of which are indistinguishable from those made at a kill. Kruuk found himself converging with lions on one of these excited groups. The attraction is primarily olfactory although the female may also advertise her condition by walking about with tail erect. Males of all ages are attracted very strongly and Deane (1962) saw as many as fifteen males. However, as the male draws close to the female there are often signs that the attraction is counteracted by fear of the female and some males may stop as they touch her and back away. Ejaculation *in vacuo* has been described by Schneider (1952) for captives and Kruuk has seen a male ejaculate over a cub and also roll in the sand and scratch ferociously when the female put her back end down a burrow. After each ejaculation over the cub the male went over to look at the female and the sequence was repeated eight times. Males attacked by the female will not retaliate but may redirect their aggression against another male. However, Kruuk remarked on the general tolerance males showed one another.

Matthews (1959) has described the reproductive anatomy of hyaenas in detail and Schneider (1926, 1952) the copulatory behaviour. When the male mounts successfully his entire underside rests on the female's back and his chin lies on her shoulder, with his back toes on the ground. Copulation lasts about five minutes and may be repeated several times. Both animals are silent. A male may stay with a female for a short time but no lengthy pair bond develops. Kruuk found evidence of a slight birth peak during the rains at Ngorongoro but some breeding goes on throughout the year.

The dens of *Crocuta* are primarily a shelter for the birth and upbringing of the young. Several females have their litters in close proximity and adult males are generally excluded. The females give birth to two, more rarely one or three, cubs after a gestation of 110 (97—132) days. During the first two weeks the mother is very intolerant of all other hyaenas and stays close to her cubs. The newborn cub is nearly black in colouring, has open eyes and weighs about 1·5 kg (Pournelle, 1965). The canines and incisors have erupted and they soon learn to walk and run and also to dig extensions to the burrow, an adaptation that presumably helps protect them from predators and larger hyaenas. Deane (1962) described a typical scene at the den.

> "On arrival at the warren a mature female with whelps down one of the holes approaches the entrance and after satisfying herself that there is no danger lowers her head into the opening and makes a purring sound emitted from the throat, at which signal the whelps will emerge. The female's arrival is treated with much excitement by the whelps, which jump all over her and affectionately lick her about the mouth, much in the manner of a litter of domestic pups. She in turn will lick them affectionately, all the time keeping up a deep-throated purr. The female will then lie down in the afternoon sun, allowing the whelps to suck greedily. Every few minutes she will raise her head and peer round to ensure that all is well. There are often as many as three females in

whelp suckling their young together, the whelps either having emerged from the same warren or, at times from different ones. The purring is kept up throughout the suckling and on the slightest sound of danger the tempo of the purring is increased to an urgent note, at which signal the whelps immediately scamper back down in the warren."

Suckling spells can last as long as four hours.

Food is never carried home or regurgitated for the young, probably because digestion begins immediately and also because many adult foods might be unsuited to the young. They therefore depend entirely on milk for about eight months and are not weaned until they are a year to sixteen months old. No other carnivore is known to depend for so long on its mother's milk. The young also depend on the mother for direct protection up to an advanced age and she will even come between them and males when they are both feeding at the kills. So aggressive are mothers in defence of their young that I have witnessed one leap at the window of a vehicle and pursue biting at the tyres. The young go through stages of following their mother from the den for steadily increasing distances until they are reaching the kills but getting little meat. There follows a long apprenticeship in which they trail along during hunts, but do not actually join in the killing until full-grown.

Spots first appear on the cubs at the age of about one-and-a-half months and they are clearly spotted at four months. Their dark legs are still noticeable at one year. They are fully mature and breeding at three years, although males may be sexually active at two years.

The genital display complete with erection first appears in cubs less than a month old and the motions of anal marking appear soon after.

Carrying a tame young hyaena in his Land-Rover, Kruuk discovered that the sight of lions did not perturb the little animal in the least but the scent of them down wind threw it into a frenzy.

In Africa, human contacts with the spotted hyaena have been widespread. In the central region of Tanzania they were sometimes reared and kept in homesteads. In Ugogo they scavenge close to the houses for refuse and excrement and commonly chew the red plastic lights off vehicles. I remember as a small boy brushing against one in the doorway of a latrine. Another hyaena had lost its right front paw and hobbled across the golf course to forage in Dodoma town. Almost every evening it would stop to rest, lying on a metal draincover below my window. Around its neck was a thin leather thong and although enquiries elicited very little factual information the local association of the hyaena with witchcraft was universally accepted. Hyaenas figure in tales of sorcery from many different areas. In western Uganda a thief cut the nose and canines off a fine specimen I had collected. Enquiries revealed that the nose is prepared by witch-doctors as a magical cure for the blind to find their way about and is also eaten to promote wisdom and knowledge. In Singida, female witches were said to ride hyaenas, as were members of the "inswelaboya" cult of secret assassins in Zululand (Deane, 1962). This author reported that hyaena eyebrows were burned to induce sleep, that burnt hair and skin were used as an emetic and that the paste of the anal glands also once had some special significance in Zulu sorcery. In Buganda, the dung used to be burnt in the laying of spirits (*amayembe*). In Karamoja and Teso the wizard (*ekapalan*) was reputed to ride a hyaena to

any village where death approached (Watson, 1950).

It is interesting that this animal should crop up so widely in Africa as the familiar of witches. Fear of the night and darkness being practically universal, it is conceivable that people exploiting this fear for their own ends might come to learn something about the behaviour of hyaenas and occasionally may have conditioned individuals of this very common nocturnal animal in order to reinforce the fear on which their status in society was built.

In many areas the hyaena is thought to have the power of transformation or to exist in two forms, one the familiar and even laughable, the other giant, ferocious and supernaturally cunning. These widespread tales may perhaps contain an element of recognition of what has been called the Jekyll-and-Hyde character of hyaenas. To the south of Mt Elgon the existence of what came to be called the "Nandi Bear" was debated for many years. Skins purporting to be those of the Nandi Bear or "chemiset", "etutui" or "kichwa mutwe" turned out to be large hyaenas.

These legends tend to be resurrected up to the present day whenever hyaenas attack people, for even in the areas where hyaenas are familiar a supernatural agency tends to be invoked to explain the phenomenon. Bouts of man-eating are known to occur, the worst period being the Uganda trypanosomiasis epidemics of 1908 and 1909 when the hyaenas became so

bold in seizing victims in the sleeping sickness camps that armed sentries were posted (Roosevelt, 1910). Also in Manyoni during 1950—51 many people were attacked at all hours. When people are eaten they seem to be treated very much like other prey.

> "Eyewitnesses stated that the hyaenas, first one and then another, taking turns, hustled the woman along as in a relay race, shrieking. Examination of the ground showed that she was devoured limb by limb on the way." (T.G.R., 1934)

That the ancient conflict between man and hyaena is not entirely a thing of the past can be seen in news items in local East African papers and reports on the 1967 drought in Turkana, when packs of hyaenas raiding villages pulled down cattle and attacked the villagers too. Sometimes the starving Turkana themselves ate the hyaenas they speared in self defence (Hillaby, 1967a).

For our ancestors, both in Africa and Eurasia, the hyaena might have been both an occasional source of food and a predator. Of greater significance man and hyaenas as successful and wide-ranging predatory scavengers must certainly have competed for food and shelter and, as people become less embarrassed by their origins, our common background with the hyaena acquires a new interest. The social and ecological strategies that underlay the success of the two species during the later Pleistocene were obviously fundamentally different. Nonetheless, as we slowly grope towards more meaningful ways of understanding human society and its development, there is a significant interest in the existence of fierce group rivalries, in the capacity to switch from individual foraging to group hunting, in a long period of exclusive dependence by the young on its mother and in other structural features of the hyaena's biology which may resemble our own.

Striped Hyaena (Hyaena hyaena)

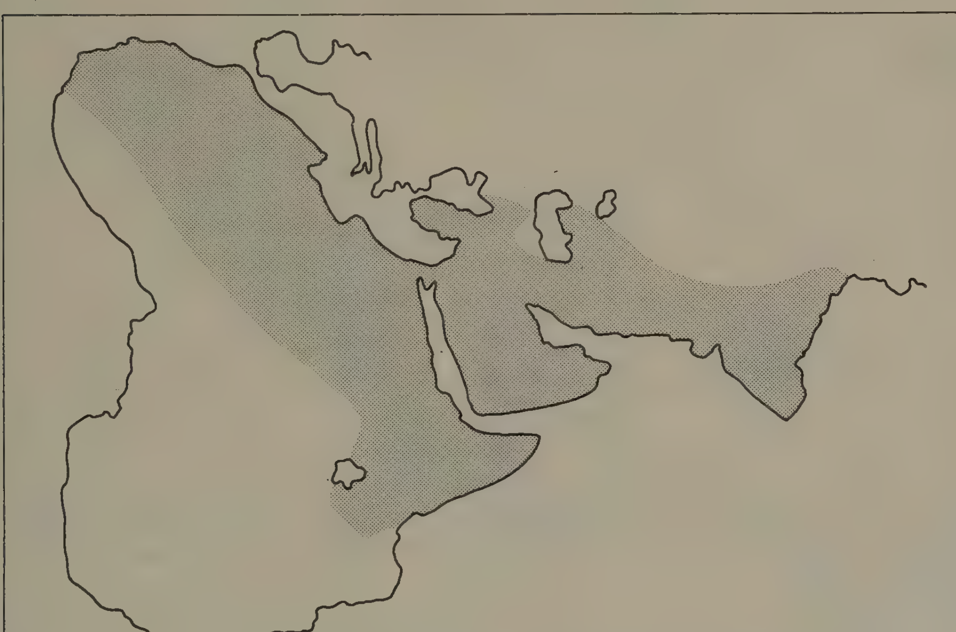
Family Hyaenidae
Order Carnivora
Local names
Fisi (Kiswahili), Ebu nagira, Ngibuin nagira (Karamojong), Didhir, Whera (Somali)

Measurements
head and body
91—120 cm
height
69—76 cm
tail
26—32 cm
weight
37—55 kg

Striped Hyaena (Hyaena hyaena)

The striped hyaena is a long-legged animal with powerfully-built shoulders and neck and typical hyaena carnassial teeth. The forefeet are very much larger than the hindfeet. A crest of long hairs runs down the back to a very bushy tail. These hairs are erected when the animal is excited and enlarge its apparent size considerably. The black face mask, throat patch and dark ears contrast with the light-coloured forehead and neck. The outer surfaces of the limbs are striped very boldly while the inner surfaces and the belly are light coloured.

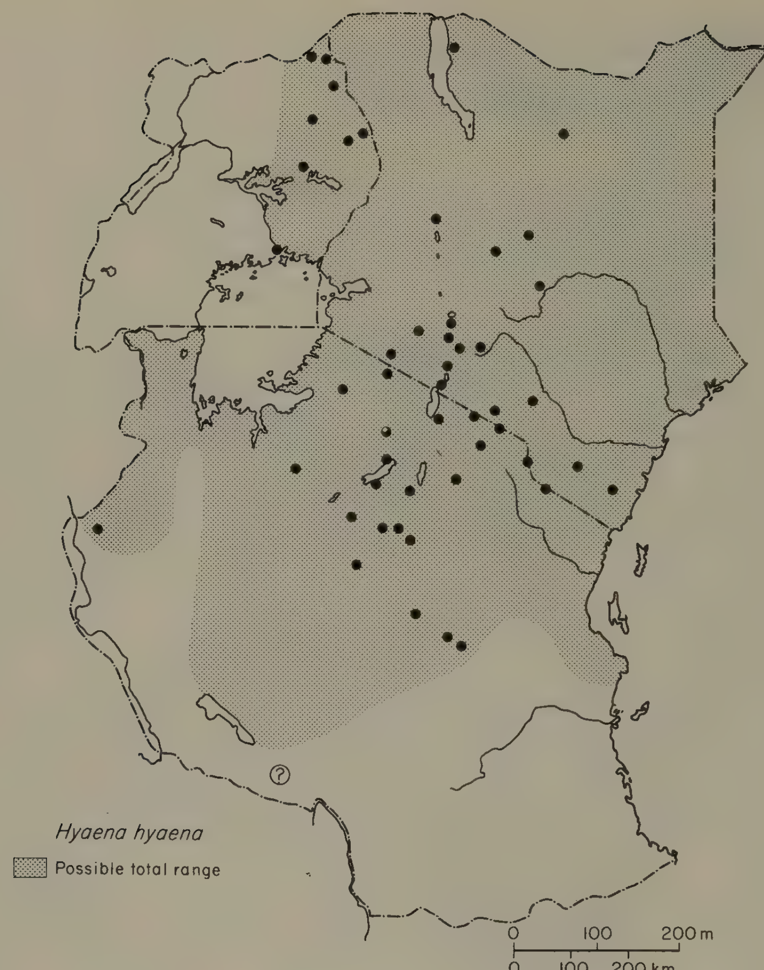
Distributed through the drier parts of northern and eastern Africa, the striped hyaena also ranged in recent years through Arabia minor, Persia, southern U.S.S.R. and a large part of India.



World distribution of *Hyaena hyaena*

They prefer dry country where their dens tend to be in stony or rocky areas, sometimes in deep caves or in burrows that they excavate themselves. Although captives drink regularly, these animals have been found in true desert and during periods when no water was available for many miles. The animals' ability to forage over great distances (for which their long legs and fast trotting gait are well adapted), may allow them to find distant water but they can probably go for long periods without drinking.

The discovery of a specimen with unusually rufous colouring from a rocky area of the Lake Victoria coast to the west of the Nile shows that this



species can live in moist conditions. (Perhaps a dry rocky locality for the home shelter is an essential factor.) It is impossible to know whether this individual belonged to an isolated remnant population pre-dating the expansion of forest along the northern shores of the lake or whether wanderers crossing lakes and rivers had come south from Teso at some more recent time. Being more strictly nocturnal, much more quiet and scarcer than its relative, the striped hyaena escapes notice very easily. It is sometimes brought to peoples' attention when it is trapped or poisoned in operations designed to control or exterminate *Crocuta*.

Examining the faeces of striped hyaenas in one area of the Serengeti, Kruuk (1975) found insects in 78% of them, fruit in 36%, birds in 44% and reptiles in 40%. Large, medium and small mammals, which are mostly scavenged, were represented by 26, 68 and 28% respectively, a much more omnivorous diet than that of spotted hyaenas living in the same area. Small animals, insects and vegetables, notably marrows and olives, have been reported in the diet of hyaenas from south Russia (Ognev, 1931). In Asia, these hyaenas will kill small stock and have even been reported to attack children.

One stomach I examined was entirely filled with a quantity of large splintered dry bones that had evidently been bleached in the sun for some time before being eaten by the hyaena; similar reports come from India. Bones are cracked with the third premolars and though the dentition is slightly less specialized than *Crocuta*'s, *Hyaena* has no difficulty in breaking up the bones of most common ungulates.

In Dodoma and Moroto, several *Hyaena* entered traps set for *Crocuta*. In these semi-urbanized localities both species are nocturnal but the entry of the much scarcer *Hyaena* into the traps implies that it is either less cautious or is quicker on the scene. As *Crocuta* is easily trapped, it is more likely that the long-legged nimble *Hyaena* tends to cover more ground and find food more quickly than *Crocuta* does. Kruuk (1975) has shown that they spend more time searching for food, 26% as against 16% in *Crocuta*. In this connexion it is interesting that Watson (1950) was told by the pastoral Karamojong, who suffer from the depredation of both species, that a striped hyaena is regarded as a pilot for spotted hyaenas, both towards beasts it cannot tackle itself and to carrion.

Kruuk (1976) has concluded that the two species have a clear mutual attraction for each other. Striped hyaenas frequently approach *Crocuta* but then show signs of fear or lie down flat in the grass; it is rare for *Hyaena* to gain any benefit from association. Numerous cases of *Hyaena* pasting on *Crocuta*-paste stalks have been observed and *Crocuta* almost invariably approach *Hyaena* when they meet and the larger species has been seen to take food from the latter or to rob its caches. With an extensive overlap in diet and feeding habits it is possible that *Crocuta* plays a decisive role in excluding *Hyaena* from the best habitats. Kruuk has suggested that the unobtrusiveness of *Hyaena* in East Africa might be a response to competition from the spotted hyaena. Without this risk *Hyaena* in Israel is distinctly noisier than its African counterpart.

It would be interesting to know whether there is any difference between the sexes in their feeding behaviour. Hamilton (1976) saw one of a pair drive leopards off their kill after which the two hyaenas appropriated the carcass and fed off it together. I noticed that a male captive belonging to Alan Root would seize its meat and retire to its den growling. The tamer female showed no signs of aggression while feeding but this might have reflected individual differences in temperament. The excreta are chalky when a quantity of bones have been eaten and digestion is evidently thorough. Excess fur and feathers is thrown up in pellets. Dung is apparently dropped at random and without ceremony.

Although striped hyaenas are reported to be strictly nocturnal, this may be partly the result of persecution. In the virtually uninhabited country east of Lake Turkana, A. Walker (personal communication) watched one out and about at 4 p.m.

Striped hyaenas wander long distances; two animals that were radio-tagged by Kruuk in Serengeti ranged over 44 and 72 sq km but this is a highly favourable habitat and it is likely that *Hyaena hyaena* in some arid areas have ranges of similar size to those recorded for *Hyaena brunnea* in the Kalahari by Mills. The brown hyaena travels 33 (11—51) km a night and the home ranges of three closely-followed females were 325, 435 and 550 sq km

(Mills, personal communication). Like *Hyaena hyaena*, the range is used by many animals and Mills caught and marked sixteen individuals within an area of 38 sq km in one year.

Striped hyaenas normally forage on their own or in pairs; both parents bring food to the young (Kruuk, 1975) and a family party may form once the young are mobile. Occasionally they congregate at a kill and up to twelve animals have been seen at a time. Even if such occurrences are not rare they are of short duration and do not imply any form of tie beyond that of the pair or, temporarily, the family. Meetings between individuals are likely to be frequent but incidental, and Kruuk (1975) has remarked on the reduction of short range bonding mechanisms in this species; for instance, there is no drawn-out meeting ceremony.

Both Kruuk (1976) and observers in Israel have seen meetings between hyaenas in which faces and necks were sniffed, followed by inspection of the protruded anus and in some cases one of the animals may lie down and expose its anal region to the other by lifting its hind leg. While following one striped hyaena Kruuk saw it encounter and chase a presumed stranger for at least one kilometre.

The vocabulary of juveniles and of antagonistic adults is similar to that of *Crocuta* but the loudest call is a rarely-heard cackling howl quite unlike *Crocuta*'s repeated whoops. Kruuk noted that striped hyaenas in Israel were louder than those he had heard in Serengeti. Short staccato whinnies or cackles signify excitement and the anticipation of food, and a quiet "hoo" has been heard between captive pairs. The juvenile want-call is almost a bleat and adults fighting utter a hoarse "aah, aah" when bitten. Threats begin with a sustained rumble, and culminate in a roaring growl and low snapping lunge. There is no curling of the upper lip and it is the lower canines and incisors that are exposed in threat. After an initial sniffing of noses, the head is progressively lowered and the initial snap is generally directed at the striped legs. Even tame captives are very sensitive to being touched on their legs and it is obvious that such slender limbs must be extremely vulnerable between the bone-cracking teeth of an antagonist. The first snaps in an antagonistic encounter force both hyaenas to fold back their paws and drop on their carpal joints and this stereotyped prelude seems to be an insurance against damage to the legs. The mouth is only opened slightly in ritualized fighting and the incisors and, sometimes, the canines are employed. Fox (1974) has described play-fights and actual fighting as highly ritualized wrestling matches with each animal attempting to seize the other on the cheek, the side of the neck or on the rump just above the root of the tail. These regions of the body are pale coloured and the well-demarcated areas of dark and light colouring, striped and plain areas seem to constitute a signal code which may help regulate social interactions through ritual. For example, the black throat is not bitten but is exposed for nibbling in an established pair, which suggests that black might have attractive connotations while the pale areas invite attack.

What has particularly struck me when watching these ritualized fights is the inversion of the usual symbolism, the aggressive animal adopting a low hunched posture with erect neck and mane while the subordinate one has a limp mane but maintains an erect stance which displays the black


ear signals
urinating
No lip curl
lower canines showing
Continuous reverberating rumble
one ear forward one back.
presenting neck for patting

throat. Also a subordinate animal sometimes backs away from a dominant one rather than turn round. As in dogs, licking of the lips, turning of the head from side to side and rolling the whites of the eyes are signs of submission, whereas a dominant hyaena has a fixed stare. The placing of the paws while resting is also significant and a nervous or subordinate animal not only carries its head very erect but also keeps its legs stretched out full length before it, while a dominant or relaxed animal folds the paws back and rests on the joints.

Following a fight or, indeed, during and after any excitement striped hyaenas extrude their anus. Brehm (1927) described the discomfiture of his polite tea-time guests when two pet hyaenas acknowledged proffered tit-bits with this display. I have seen a wild hyaena extrude its anus when about to seize bait and also when approaching another hyaena. Fox (1974) noted that during the infrequent social investigations of captives it was the peer that

extruded the anus for five to ten seconds, while the other sniffed. After fights it was the subordinate animal that consistently extruded, and Fox concluded that the action was appeasing in function.

This conclusion can probably be extended to the action of smearing a grass stem with deposit from the anal gland. I saw a male that had been released for the first time into a large enclosure with a female chased to exhaustion by the female. After a fight in which the female got her teeth into his rump and held on, he took refuge in the corner near his own pen and started to mark a grass stem. The female approached while the anus was still extruded but her interest was in the mark rather than the marker. After smelling the stem very carefully, she adopted a more friendly approach to the male, which had remained with lowered haunches.

The sex of an animal making an anal deposit probably influences the reaction of other hyaenas encountering it. I placed tufts of grass that had

been marked by wild hyaenas in the pen of a captive pair. One deposit excited both sexes; the female in particular made small puffing movements of the lips while the cheeks acted like bellows and the animal appeared to be sampling the aroma by blowing and sucking air over the globule of secretion. She then licked the deposit very gently without disturbing it and guided the grass stem down the throat as she moved forward. With an elaborate lift of the forearm and then a hindleg, the stem was run down the belly to be carefully and firmly smeared by the extruded anus. This is a highly ritualized sequence which is always followed by a hyaena marking a grass stem.

Another deposit by a wild hyaena was cursorily sniffed at by the same female, instantly marked and then ignored. The stem now carried two globules. It was examined by the male very slowly and carefully with his ears back. Frequently licking his nose, he smelled up and down the stem several times but did not make any attempt to superimpose his own mark. Kruuk (personal communication) found that deposits were apparently made at random throughout the home range but he found that dung deposits had a more peripheral distribution. In the light of *Crocuta*'s clan territories it would be interesting to know whether the members of a regional population of *Hyaena hyaena* are more intolerant of outsiders than they are of one another.

Apart from man, his poison and his dogs, against which they have no effective resistance, very little is known about controlling factors but their very low density probably protects them to some extent from the worst effects of predation, competition and disease, while large home ranges must help them mitigate adverse changes in their habitat. Periodically in the past they were reported to have become unusually common in parts of India but no reason for this was advanced.

There are few published accounts concerning reproduction and courtship but Ognev (1931) reported that oestrous females may be followed by up to three males. Fox (1974) noted that it was the male of a captive pair that was subdominant and I have witnessed unequivocal dominance by a female captive over a slightly larger male. It would be very interesting to learn if the female makes a choice among her suitors and how a pair is formed, for it appears that bonds are sustained into the period of rearing young, both parents bringing food back to the den.

Gestation is said to be three months and the number of young ranges from one to six, although two to four are more common. When new-born, they are less advanced than *Crocuta* cubs, being blind and helpless. They are little miniatures of the parents and do not exhibit distinct natal coats. In captivity, males show no antipathy to the young and there is not the long period of dependence on the mother's milk found in the spotted hyaena.

In captivity males show no antipathy to the young and wild males visit the den alone or with the female.

Kruuk (1976) observed regular suckling visits by the mother which generally took place at nightfall but were also frequent around midnight; juveniles of up to one year would suck. He also saw mothers carry meat back to their offspring in the den and even a one-and-a-half year old hyaena was seen to carry a gnu leg over two kilometres back to the family den. The young accompany the adults at about six months of age.

Aardwolf, Proteles (Proteles cristatus

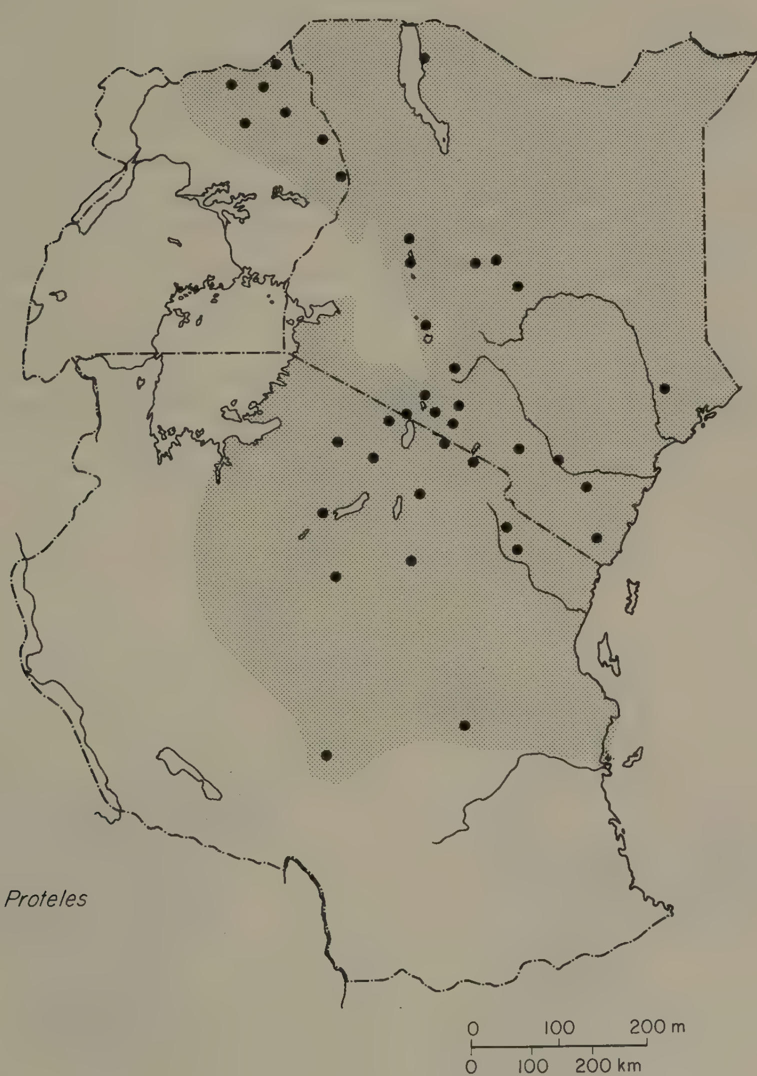
Family Hyaenidae
Order Carnivora
Local names
Fisi ya nkole (Kiswahili), Lalur, Tindilio (Lwo), Ebu napanaethe (Karamojong)

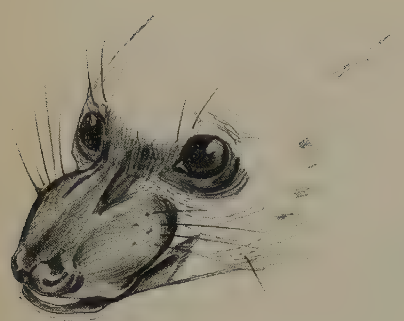
Measurements
head and body
55—80 cm
height
48—50 cm
tail
20—30 cm
weight
10 (9—14) kg

Aardwolf, Proteles (Proteles cristatus)

Proteles is one of the indicator species for the Somali—Kalahari semi-desert axis and is one of the numerous forms of arid-adapted fauna and flora that neither inhabits the Sahara nor any part of its margins. Considering the vast area of this desert this biological anomaly is rather surprising.

Darlington (1957) defined the fauna of the Sahara as very limited and specialized, with some Ethiopian and some Eurasian relationships. Moreau (1966) pointed out that during a long period in the late Pleistocene a Mediterranean type of *macchia* vegetation extended to what are now the southern margins of the Sahara. This probably tended to favour Eurasian fauna and only the more adaptable of the Ethiopian elements.





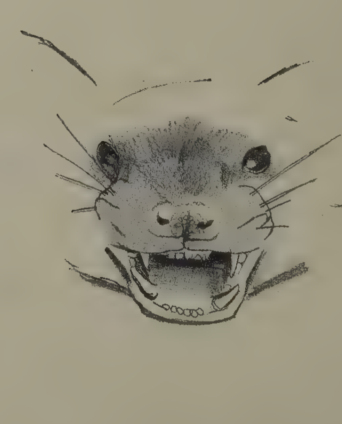
As was pointed out in Vol. I (p. 63) the Horn of Africa and South-West Africa have probably had dry climates for some ten million years, encouraging the evolution of numerous endemic species. Occasional semi-arid corridors have allowed circulation of the less strictly arid-adapted species between the two areas while the Ethiopian mountains and the sea have tended to restrict the emigration of endemic fauna and flora out of this long established north-east—south-west axis.

The restricted distribution of *Proteles* is almost certainly directly connected with the ancient climatic history that has bequeathed a general biological poverty to the non-forested areas of western Africa (see Vol. I, pp. 80—81). For instance, Hoyle (1955) has estimated that the plant species may be only one fifth as numerous as in East Africa. This biological impoverishment appears to embrace the termite genera on which *Proteles* is dependent and it has been pointed out that in West Africa harvester termites are relatively less numerous and prefer bushier habitats than in southern and eastern Africa (Kruuk and Sands, 1972).

Proteles are most readily seen on dry plains where harvester termites, *Trinervitermes*, *Hodotermes* and related genera reach a very high density and emerge from their underground nests at night to feed on grass. The abundance of these surface-foraging harvester termites is known to increase very greatly with heavy overgrazing (see the profile of *Orycteropus*, Vol. I, p. 381; Coaton, 1948 and Harwig, 1955), which explains why *Proteles* is particularly common in some areas where there are many wild ungulates or domestic stock. Where these termites are rare or absent so is *Proteles*.

The most immediately striking features of this delicate, striped animal are its large eyes and ears, the peculiar form of its naked leathery muzzle and the crest or mane of extremely long erectile hairs that runs from behind the ears to the tail.

In the Serengeti National Park, Kruuk and Sands (1972) watched *Proteles* searching for food. Hearing and, possibly, scent guide them to dense con-



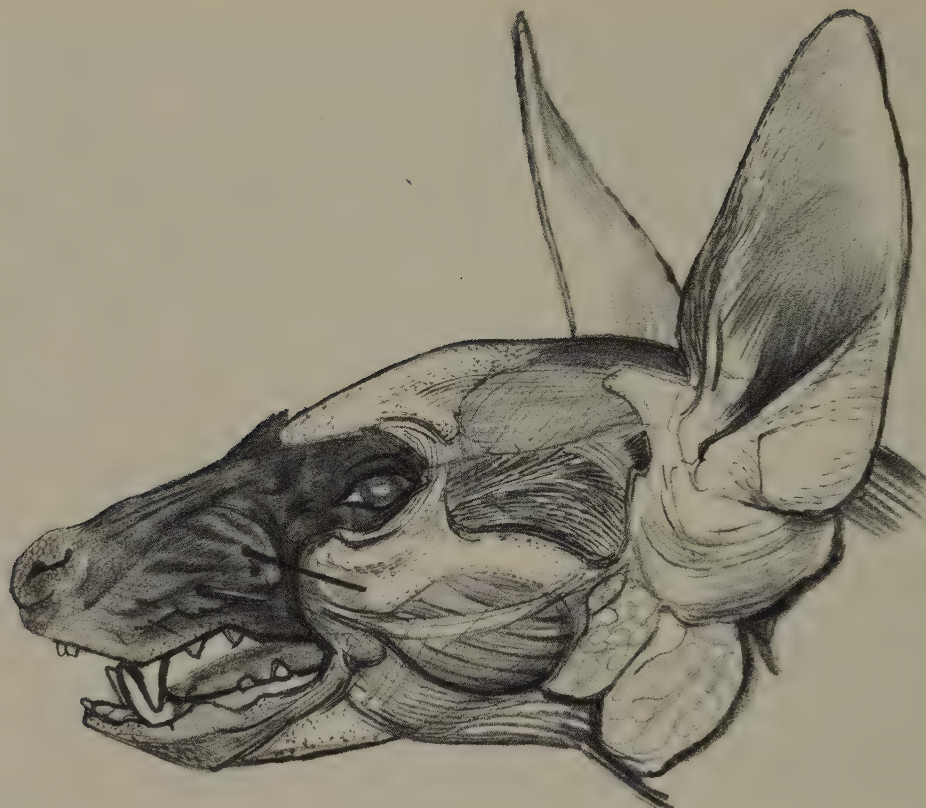
centrations of *Trinervitermes*, which are usually lapped up in less than half a minute, after which the animal passes on. These authors noted that termites are never found downwind; instead the commonest prelude to feeding is a sharp turn upwind. The animal appears to listen intently before it moves and starts to feed, and its maximum range for locating insects is about two metres. Although there are frequently very large numbers of *Trinervitermes* remaining after *Proteles* has passed, these are mostly soldiers and Kruuk and Sands suggested that the chemical defences of this caste might deter the predator, particularly once the soldiers outnumber the workers. It is interesting that the ground pangolin, *Manis temmincki*, and some other termite-eating animals have been observed to avoid this species, the soldiers of which squirt chemical secretions from their pointed heads (hence the name snouted termites).

Of five stomachs examined by me all contained snouted termites and only one had also a few small grasshoppers.

Ants, beetles and their larvae, moths and other insects as well as spiders have been recorded. Bothma (1965) found the remains of a rat and a very small leopard tortoise, some green grass and a quantity of carrion as well as a few insects in the stomach of one Transvaal aardwolf but of five other stomachs the bulk consisted of *Trinervitermes* species.

Records from a hundred stomachs in South Africa revealed only termites and insects (Fremer von Ketelhodt, 1966). Shortridge (1934) listed rodents, reptiles, nestlings and eggs of ground-nesting birds; even ostrich eggs are reputed to be opened by knocking them against one another. A captive juvenile killed 26 pigeons and francolins in an aviary, of which a few breasts were slightly eaten (Fremer Von Ketelhodt, 1966) and honey is also favoured by captives.

The lapping up of termites is facilitated by extremely rapid tongue movements and a coating of rather sticky saliva supplied by the very large salivary glands. Soil inevitably gets ingested but there are conspicuous regional and perhaps seasonal differences in the amount of soil in faeces. The animal generally feeds standing but occasionally may drop on to its knees.



Young wart hog lower jaw

Proteles lower jaw

Wear on the front of the lower incisors of most adults betrays that feeding is not only accomplished by licking and the rather spade-like form of the lower jaw has some resemblance to the mandible of a young warthog (see margin)!

One stomach that I examined contained about one kilogramme of termites with very little earth and it has been estimated that *Proteles* can gather 40,000 termites in less than three hours; a young captive fed on 1·5 kg of termites a day (Linley, 1965).

Termites are a rich source of protein and fat and Fremer Von Ketelhodt noted the flesh of an aardwolf as being so fat as to be yellow. This author noted that a captive stayed in its den for up to 48 hours after feeding well and, on milk and termites, could subsist on five meals a week; it only emerged into the open when hungry or in order to sun-bathe for a couple of hours during the morning. Linley (1965) also confirmed that a well-fed aardwolf will not show itself for a couple of days. These observations suggest that *Proteles* exposes itself as little as possible; it also suggests that even in a nocturnal animal with a very rich diet, sunshine might play an important role in its physiology.

On Serengeti, Kruuk and Sands saw *Proteles* foraging during daylight but noticed that it hunted along the edges of high grass patches where the termites came to the surface under the cover of vegetation. After dark there is a more general dispersal of termites and also of *Proteles*. In this area Kruuk

found that *Proteles* were spaced out one to two kilometres apart and pairs might share a home range. He did not see overlaps in home range and once observed two animals avoid one another exactly on the boundary of a known range. He also found that scent deposits from the anal glands appeared to be the main means of boundary marking, although their marking is associated with excitement and can occur anywhere within the home range. Kruuk and Sands saw bouts of marking activity, anything between five and twenty marks being made in as many minutes. The orange secretion is squeezed out on to a grass stem from the anal protrusion during a quick lowering of the rump. Both sexes mark and have equally well developed sacs. The secretion is not unpleasant but is extraordinarily long lasting and I found that small gobs of it left on a skin still retained their scent after three years.

Whereas the hyaenas use dung latrines as boundary markers, the home range of a *Proteles* contains four or more scattered latrines. Kruuk and Sands saw animals walk several hundred metres to defaecate in the nearest deposit, which was sometimes on a gnu's stamping ground, and I have found one on an old flower bed. The dung deposit is dug into before a new defaecation and the animal rakes earth and old faeces over the dung with its forepaws before leaving. Fremer von Ketelhodt found that both sexes used the same deposits, sometimes urinating there as well and he found one about 30 metres from the entrance to a den. A satisfactory explanation for the function of latrines awaits more detailed study but in a home range that is without paths they are, like the den, landmarks that are frequently revisited.

Proteles are generally observed singly or in pairs and considering the scattered nature of their food it is obvious that they are primarily solitary animals. However, several females have been found together with their young in one earth and Lanham (in Shortridge, 1934) saw as many as fourteen together in the Kalahari. It is interesting to find this evidence of sociability on the part of an animal that can gain no nutritional advantage out of it.

Although natural holes and *Orycteropus* burrows may be used, captive *Proteles* have proved themselves capable of digging their own holes in soft soil.

Young *Proteles* are sometimes playful, darting about and waving their tails like a jackal. Their reactions to sudden movements and noises are immediate, but in spite of being shy they do not always run far and often turn back to watch the source of disturbance with raised ears and head. If chased, they zig-zag about and make for the nearest hole. Postures, particularly in defensive displays are exaggerated and the tactic of dropping on to their knees like *Hyaena hyaena* has been observed. Expression in the face is mainly limited to the ears and eyes and opening and closing of the mouth, for the rather leathery lips are unable to assume the pouting, grinning or snarling expressions of dogs and cats and, to a somewhat lesser extent, hyaenas. The mane on the neck is capable of being fanned independently of the dorsal crest, thus giving a special emphasis to the head, while the simultaneous erection of both makes the animal appear twice its size. When erect, the banded hairs delineate bold horizontal stripes in contrast to the vertical banding of the body. This probably serves intraspecific display, but the little animal can bluff with the greatest ferocity when brought to bay and Cloete (in Sclater, 1900) described one making a kind of roar, ending in a yell as it charged his dogs. Although almost wholly silent as captives, a variety of

calls has been described for these animals in the wild; Wilhelm (1933) said that they have a howl similar to that of a striped hyaena and Langden (in Shortridge, 1934) heard them "whistling to their mates". When dug out of their burrows or baited by dogs they growl and grunt defensively. Smithers (1966) has described a thin bark like a dog's.

A small defenceless animal living in open habitats, the aardwolf probably suffers similar dangers to those of jackals. They are recorded victims of python and leopard as well as domestic dogs. The suggestion that *Proteles* might mimic *Hyaena hyaena* has been discussed earlier.

As was already pointed out, aardwolves can thrive where cattle are ranched intensively and it is conceivable that their activities might actually reduce the damage done to grazing by harvester termites and they certainly deserve the formal protection that they are supposed to enjoy. They provide headdresses for the Karamojong and medicines and meat for some South African peoples. They are sometimes the target for local furriers; I have seen a kaross containing nine skins.

It is doubtful if competition for food resources affects *Proteles* very much. Brockman (1911) suggested that aardwolves might follow *Orycteropus* for the leftovers. While such gleanings might help out during times when surface dwelling harvester termites were scarce this is not a regular source of food.

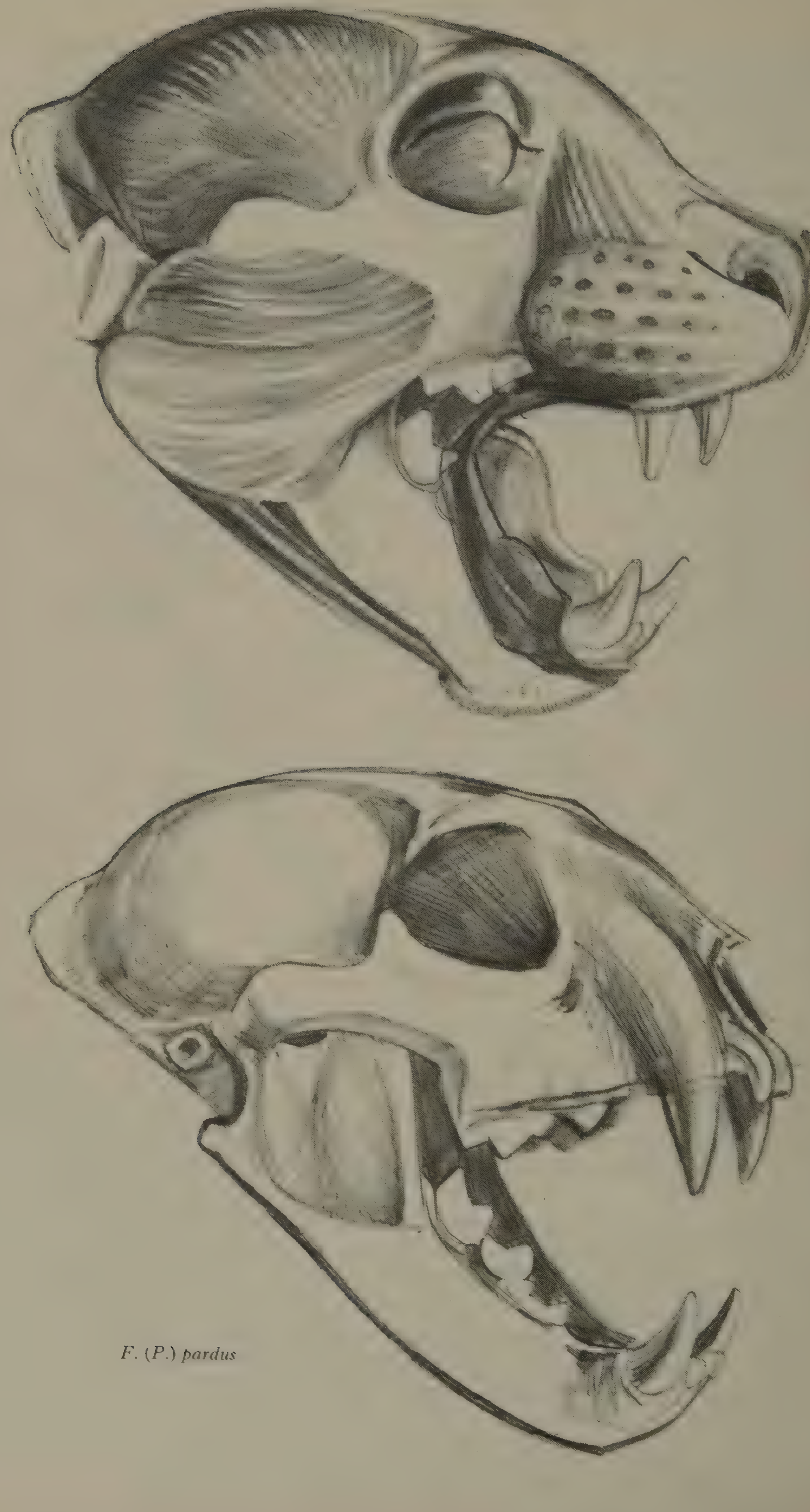
Both sexes appear to be of similar size. Nothing has been published about their sexual behaviour but gestation is thought to be about three months (90—110) days. I picked up a run-over female in southern Kenya that had

just given birth at the end of May. Her mammary glands were exceptionally large and contained plenty of milk. She was stained by the red earth of her burrow. A juvenile, probably several months old, was run over in Uganda in July.

The young generally number two or three (one to five) and Shortridge (1934) suggested that records of larger numbers might represent two litters in one den. They are born blind and helpless. Fremer von Ketelhodt stated that both parents care for the young but did not elaborate. A pup estimated to be about 25 days old weighed 350 grammes. Captives reared by Spinelli (1970) and Linley (1965) thrived on cow's milk.

Linley reported that at about two months the aardwolf was 203 mm at the shoulder. Fremer von Ketelhodt reported a young captive sleeping during the day and drinking in the late afternoon. As this juvenile grew up, it demanded a drink of milk between eating termites. This author suggests that parents regurgitate food to the young.

It is not known at what age the young become independent but adult size seems to be reached by the age of about nine months.



F. (P.) pardus

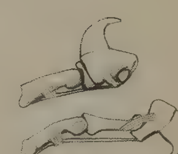
Cats

Felidae

Felis (*Felis*)
Felis (*Panthera*)
Acinonyx

Like the other Carnivora, cats emerged from the miacids but their earliest history is uncertain and the first recognizable felids are sabre-toothed cats in the Upper Eocene. Because of this many authorities believe that the modern cats have derived from some form of sabre-tooth.

The genets, *Genetta*, parallel some aspects of the cats' earlier origins as predatory climbers but the large Madagascan fossa, *Cryptoprocta*, is an even better example of a cat-like viverrid and events lost in the Eocene may have been recapitulated more recently in Madagascar. Simpson (1945) regarded *Cryptoprocta* as a survivor from a period when cats and viverrids were closely similar. An ability to extend curved claws from a neatly folded position presumably predates the emergence of the living families, and both felids and arboreal viverrids have inherited this structure, the mechanism of which is illustrated opposite and in the profiles. For most cats, however, the climbing function of claws has been overshadowed by their role as meat hooks.

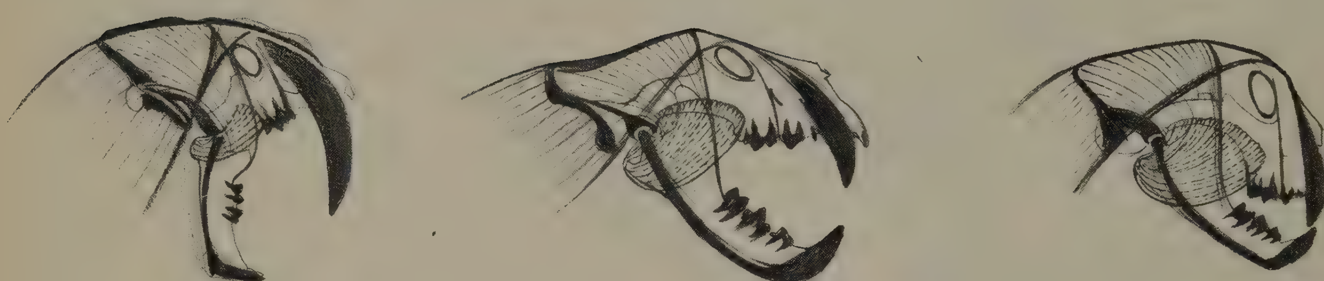


Of all the carnivores cats are the most efficient killers. Clawing into their prey, they quickly fasten their teeth to whichever part of the body is more vulnerable and will lead to a rapid death. Thus a lion may enclose a gnu's nose with its own mouth and smother it, a leopard may bite at the nape of a cane rat and dislocate its spinal chord or a cheetah strangle a gazelle by clamping into its throat. In collective killing by prides of lions each of these holds may be practised on the same victim. Where a variety of prey species are eaten the cats sometimes learn by experience to adopt the most appropriate slaughtering technique, but Leyhausen (1956) has demonstrated that there are specific peculiarities in killing behaviour and, more important, that all felids are adapted to bite with great accuracy.

These details have some reference for the cats' controversial ancestry. Accuracy must have been particularly crucial for the extinct sabre-tooths because the long sharp canines were only adapted to slash or stab in relatively soft tissues. Since prey was almost certainly very much larger than the sabre-tooths there would have been a strong selective pressure for cats capable of disabling their prey with the minimum of effort.

The efficiency of an aimed bite by a modern cat might be the legacy of a sabre-tooth predecessor. Furthermore, a long skull could never have provided the base for an accurate and forceful strike with the upper canines and sabres can be correlated with a very short skull and a reduced tooth-row (Ewer, 1973). If extreme shortening of the face was directly contingent upon the development of sabres, then the modern cats almost certainly derive from one or other of the sabre-tooth lines. On the other hand , if shortening of the face was an independent development which allowed the canines to elongate enormously in some lineages while more normal jaws were retained

in others, then the modern cats might derive from the latter. Cats are primarily distinguishable from sabre-tooths not only by the relative size of their canines but by the involvement of the lower jaw in the killing bite. Romer (1945) has pointed out that not all sabre-tooths developed stabbing teeth and he suggested that the smaller, less specialized Oligocene form, *Dinictis*, could have been ancestral to the modern cats in *Felis* and related genera.



Diagrams indicating differing functions in felid skulls and skull musculature.

1. Stabbing strike (*Smilodon*, sabre tooth).
   Strike by enlarged upper canines. Principal force exerted by neck muscles. Diminutuve masseter.
2. Canine bite. *F.* (*P.*) *leo*, lion). Deep pincer action by long canines in both jaws. Neck and jaw muscles well developed.
3. Clamp stranglehold (*Acinonyx*, cheetah).
   Sustained jaw clench by short bunched jaw muscles. Clamp action enhanced by steepened facial angle and downward bend of maxilla on basi-cranial axis

Ewer (1973) has pointed out that the appearance of Felinae in the fossil record coincided with the rise of fast modern ungulates. The earlier Felinae might have been adapted to delivering what she calls an "occipital crunch" on small to medium-sized prey and she has proposed that speed and hunting skill might have been the key to the ultimate displacement of sabre-tooths by modern big cats.

If the feline antecedents were small, primarily forest-dwelling animals many members of the cat family could be metaphorically described as following their prey out into more open country, for such an hypothesis is in accord with the history of several major groups of mammals and has some support from the distribution and morphology of modern felids, which show some very interesting gradients in size and habitat. These are discussed at the end of this profile.

The general characteristics of the felid head as well as some specific traits are well exemplified by an examination of the cheetah, and I have already illustrated the rather geometric disposition of functional activities in this skull (Vol. I, p. 94).

The face and muzzle are almost as steeply sloped as a sabre-tooth's; the jaws do not open particularly wide because the premium is upon short jaw muscles which are capable of maintaining an unrelaxed throttle hold for up to twenty minutes until the prey has died of suffocation. This killing technique probably explains a rather striking peculiarity of the muzzle. The nasal aperture and the passages behind are exceptionally large. Since a successful chase ends in a stranglehold, the cheetah must recoup its oxygen debt while holding the prey down and with its jaws firmly clamped into the animal's throat. Instead of resting and panting through an open mouth, the cheetah must maintain muscle tension and only breathe through its nose, and it is probably during this period rather than during the chase itself that a wide clear passage for rapid breathing is needed.

Cheetah teeth illustrating slicing action

Narrow, sharp-bladed cheek teeth typify felids and the only functional teeth behind the canines are the upper premolars 3 and 4. These scissor down across the blades of premolars 3 and 4 and molar 1 in the lower jaw giving a slicing action and in many species they have little ability to break up bones. Indeed, cheetahs tend only to strip the meat off their kill, to which they do not return. A striking peculiarity of the cheetah's skull is inflation of the inter-orbital area to create an extensive trapezoid-shaped air sinus in the area between the eyes and above the cribriform plate. This empty chamber has a broad flat top but the effect is to steepen the angle of the face and of the front of the zygomatic arch, elevate the eyes and increase their distance from the toothrow. It slightly enlarges the canopy above and behind the eyes (where it could conceivably act as a sun-shield) and the chamber lightens a skull that is already light for its size. Elevation of this middle portion coincides with an extreme reduction of the toothrow; this effectively shortens the length of the skull relative to its height, and it is possible that this change of proportions improves the jaws' clamping action. It might also enhance bifocal vision but this is likely to be a subsidiary function to that of improving the mechanical advantage of the jaw muscles.

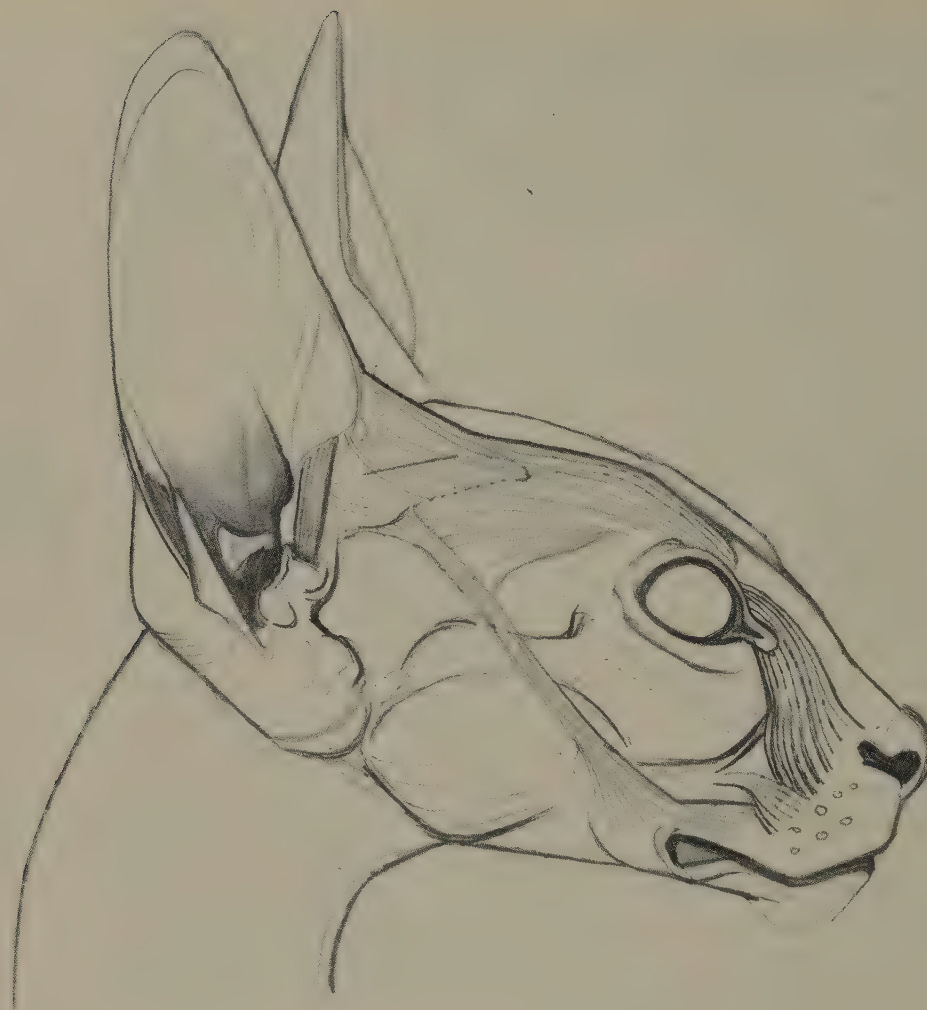
It is interesting that the cheetah's black "tear stripes" tend to emphasize the species' most distinctive structural feature, the verticality of its face (see pp. 304, 406) and link the mouth and eyes which, in this species, play a more significant part than the ears in expression.

For many cats the ears are of great importance, not only for hearing but as signals and they are served by muscles which are particularly well-developed in some species. (The drawing overleaf illustrates a serval cat.)

Cats have the most expressive faces of all carnivores. Their short muzzles and bifocal vision are obvious adaptations to a wholly predatory life, but a world-wide anthropomorphization of cats has been assisted by a man-like facial format and repertoire of emphatic expressions.

The genus *Felis* is known from the Pliocene in South Africa and might go back to the late Miocene in Eurasia. *Acinonyx* is known from the early Pleistocene in Europe and Asia in the form of a particularly large race. *Felis* (*Panthera*) is abundant in the Pleistocene African deposits and it co-existed with various species of sabre-toothed cats, *Megantereon*, *Machairodus*, *Therailurus* and *Afrosmilus*, (Savage, in press).

The sabre-tooths disappeared at the same time as the primitive elephants (notably the mastodons) which was relatively early in Europe and late in



America. Romer (1966) has suggested this was a case of the predator going out with its prey. The sabre-tooths were an extreme case of specialization but some of the large living felids are also relatively inflexible in their diet. Fruit, insects and very small animals are occasionally found in the stomachs of some smaller species but the cats are generally dependent on abundant populations of appropriately sized prey.

The reduction of wild herbivores has inevitably resulted in the decline or extinction of their feline predators and the widespread retreat of the big cats in Africa is primarily due to this limitation. Epidemics of feline diseases may have a strong local influence and trapping for skins a more general one, but neither are likely to have a decisive impact where prey is abundant and the animals are well spaced out in their territories.

Most felid species live a fundamentally solitary existence, each animal having a hunting range that overlaps that of its neighbours. Fights are probably quite frequent but these serve to reinforce a system of mutual avoidance, which only breaks down when there is the very strong counter attraction of sex. Where there is a social system, as amongst lions, this appears

to be an elaboration of the family. However, homosexual or pseudosexual behaviour is frequent in lions (and in some cheetah groups), which suggests that antipathies are more easily suppressed by resorting to a behaviour that is typical of courtship.

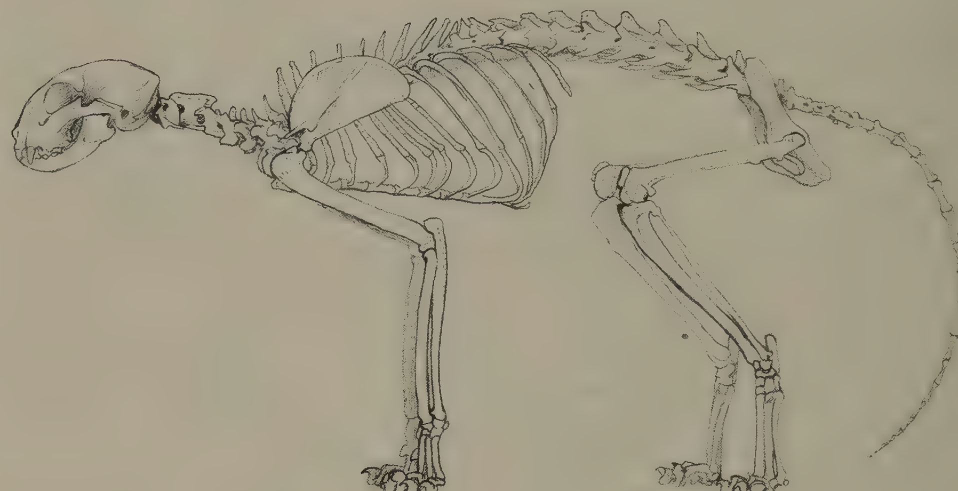
Behaviour that has been diverted from its sexual origins has a more profound and general significance for cats. The efficiency of their killing could constitute an obstacle to social relations for predatory carnivores that maintain exclusive hunting grounds. It is probably because all intraspecific contacts amongst intolerant animals have a real element of danger that the cats have evolved elaborate appeasement behaviour. Hindquarters are presented in a gesture which is typical of many mammals and is generally thought to have sexual connotations. The posture is sometimes emphasized by lowering the forequarters and all cats raise the tail vertically and twitch or shiver it. In many species the tail attracts attention because it is barred or spotted; the upper surface may share the body's ground colour but the tip and underneath are lighter and have stronger contrasts. The inner surface of the limbs, belly and throat have similar colouring and it is significant that these areas are almost totally hidden in the stalking posture and in aggression but become eye-catching when the cat makes the ultimate appeasement gesture of rolling on its back and exposing its underside. This action is further advertised by squirming on the back while the animal miaows or purrs. Cheetahs resemble dogs in their tendency to intersperse such servility with bouts of romping play and mutual licking. Elements of appeasement typify most felid greetings and are often seen in direct response to a growl or threat.

Dominance or threatening behaviour is the opposite of appeasement and is broadly similar for all species. The animal tends to assume a lateral stance, stands very tall, arching the body and tail and fluffs out its fur, while it faces its opponent and snarls, spits, roars or lunges out with an unsheathed forepaw.

Facial ruffs, dorsal crests and well-furred tails are all devices for increasing the apparent size of an aggressive animal, and facial expressions are systematically enhanced by subtle tones and markings on fur and on the skin of the nose, eyelids and lips. These patterns are usually specifically distinctive and small variations may allow the recognition of individuals but they must also contrive to render the animal inconspicuous during a stalk or during the long hours of daylight rest.

Almost all cats are primarily nocturnal and depend on cover both for shelter and effective hunting; their highly developed facial vibrissae are an adaptation for easy passage through dark undergrowth. The most notable exception is the cheetah, and it is interesting that this species has poorly developed whiskers with insignificant innervation through the infraorbital canal. Its long limbs are an obvious adaptation to fast running but the cheetah remains a cat in that it stalks whenever it can and is incapable of sustaining more than a single short dash. A cheetah is sometimes less agile than its prey and relies above all on speed to overcome it. This was once demonstrated to me in a vivid fashion when an impala came racing over a rise and avoided my stationary vehicle with a sideways leap. The cheetah, which was on its heels only avoided collision by leaning over sideways to such an extent that it skidded on to its sides, scraping fur and skin in the process. Hopwood (1947b)

showed how the muscles controlling fore-aft movement in the shoulder, the *serratus magnus* and *levator anguli scapulae*, have a deep concentrated insertion on the inner surface of the scapula, whereas the leopard has a versatile and mobile shoulder with more diffuse muscle attachments. The cheetah's limbs show modification for running in every detail of their structure (see drawing), Hildebrand (1959, 1960) has analysed the gait in detail.



Skeleton of *Felis sylvestris*. Left, above: forearm of cheetah (*Acinonyx*). Left, below: forearm of golden cat (*F. aurata*)

All cats have a tendency to climb into particular trees or on to elevations, which are marked by raking their claws, by urine or by dung, according to sex, status or species. These viewpoints probably serve several functions in their territorial and social system and the particular emphasis may vary somewhat with the species (see pp. 349 and 404). Viewpoints involve the felids' two key senses, vision and scent. They generally hunt by sight alone but their social life is regulated by visual, olfactory and, to a lesser extent, by vocal signals. Like urine or anal marking in other carnivores, the creation of scent posts appears to be essential for a confident relationship with the environment and for indirect contact with neighbours and transient conspecifics.

The importance of scent marks has been demonstrated very well with domestic cats, for males will not normally mate in strange surroundings and even ignore an oestrous female until they have explored, scratched and urine-marked. However, Michael (1961) has remarked that tom cats will mate in totally strange surroundings if a familiar human is present, which implies that merely by his presence a keeper can transform the surroundings into an acceptable scene.

For the female cheetah a new litter signifies a new cycle in the animal's relationship with her environment and Adamson (1969) noticed that the marked trees and termitaries favoured by one family were abandoned when it dispersed and entirely new viewpoints were adopted by the same female with her next litter.

Thus there is a social connotation to viewpoints which must vary with the condition of an individual as well as from species to species. For lions, claw-scarred or scent-sprayed trees are themselves a stimulus for further scratching and squirting, and Adamson's hand-reared lions never passed an established scent-post without a marking ritual. Schaller (1972b) listed additional situations in which lions spray and scrape. The commonest context follows an encounter with another lion, whether this is friendly or aggressive, and it is also seen after a disturbance by another predator such as a hyaena or a vehicle. It is commonly elicited by the presence of an oestrous female and also occurs just before departure for a kill. Schaller often saw males rub themselves on spots that had been previously squirted at by another pride member and he remarked that the pride might acquire a characteristic odour in this way. Here again there is the implication that an important feature of any experience or encounter for a felid is that it should have a familiar smell.

The face rubbing that accompanies cat greetings might also involve the transfer of scent. It is often associated with copious salivation or licking and, while this might have the utilitarian function of cleaning bloody faces, it is often associated with and might be stimulated by situations that call for appeasement. Amongst lions, Schaller found that the most frequent rubbers were cubs to females or both to males but the latter seldom rubbed other lions. That cats may respond only to the scent of a dominant animal is suggested by the fact that a female domestic cat will start submissive rolling when brought into the presence of a male even if she is unable to see or hear him (Michael, 1961). Both male and female cats indulge in bouts of restless activity during which they rub their heads on every object within reach. In the case of females this is correlated with the onset of oestrus (see pp. 327, 385). The behaviour is either triggered internally or else it is possible that the animal is stimulated externally by the smell of its own secretions. It is interesting that the cats' response to catnip and valerian is indistinguishable from oestrous behaviour (Palen and Goddard, 1966). That unusual activity on the part of male domestic cats may be influenced by hormonal changes is given some credence by the discovery that not only are the females seasonally polyoestrous but that there is a latent sexual cycle in male cats which corresponds with the female's cycle (Aronson and Cooper, 1966). If such cycles occur in wild felid species, this could have far-reaching implications for our understanding of their biology.

Outside the breeding season, females are not only intolerant of other cats, they are themselves repellent, and domestic toms will turn away sharply after smelling a female out of oestrus (Michael, 1961). Both partners exhibit sudden changes of mood during courtship, and submission by the female may alternate with fierce repulses and copulation is sometimes a tense and, for the female, apparently a painful affair.

All cats give birth to blind and helpless young generally in a well-hidden

retreat. Fed at first on milk and then weaned at the kill, the young only learn to hunt for themselves rather slowly. When they are eventually rejected or become independent, the young of all species go through a trying period. Inexperienced at hunting, they are probably driven into a nomadic phase by the intolerance of established territorial adults. In terms of selection for survival this is perhaps the most testing period in a feline's life.

The big cat species are fiercely intolerant of one another. Lions chase and kill leopards and the latter have been recorded killing cheetahs and chasing serval cats. In these encounters they appear to treat the other cat more like a strange conspecific than a prey animal. The question of competition between felids may be of the greatest significance for their evolution. For example, the behaviour and even the presence of leopards may be conditional upon other large cats. In the absence of lions and tigers, leopards are generally less restricted ecologically and may become more terrestrial. They are bold and common in the moist, cold alpine regions of the Ruwenzori Mountains. Immediately below, in the mixed but densely vegetated subalpine zones golden cats are abundant. The latter species is absent, or so rare as to be insignificant, in equivalent habitats on the Aberdares, which are drier mountains with direct access to the plains, not entirely surrounded by a forest barrier and where there are, instead, numerous serval cats. Above this zone, the alpine moorlands are dominated by lions and the leopard is found in the forest and mixed habitats. Even on the most superficial acquaintance the leopard's ecology and behaviour evidently differ on the two mountain massifs.

Whether through the agency of geography or climate, isolation allows a species to make a local accommodation to different conditions and to the presence or absence of competitors. In larger areas and over prolonged periods it provides the basis for speciation.

The local situation on the Ruwenzoris has an equivalent in the vast woodlands and tundras of Siberia, which would appear to offer habitats well-suited to the leopard. The former pre-eminence of Siberian tigers not only could explain the absence of leopards but could also suggest that the tiger itself might have emerged through the isolation of a leopard-like stock in a habitat rich in large ungulates and free of competition. The fact that tigers did not reach America whereas the leopard-like jaguar did (becoming heavier and slower than its Old World relative), suggests that their evolution might have been relatively recent. The attribution of East African Pleistocene fossils to *F.* (*P.*) *tigris* is very dubious.

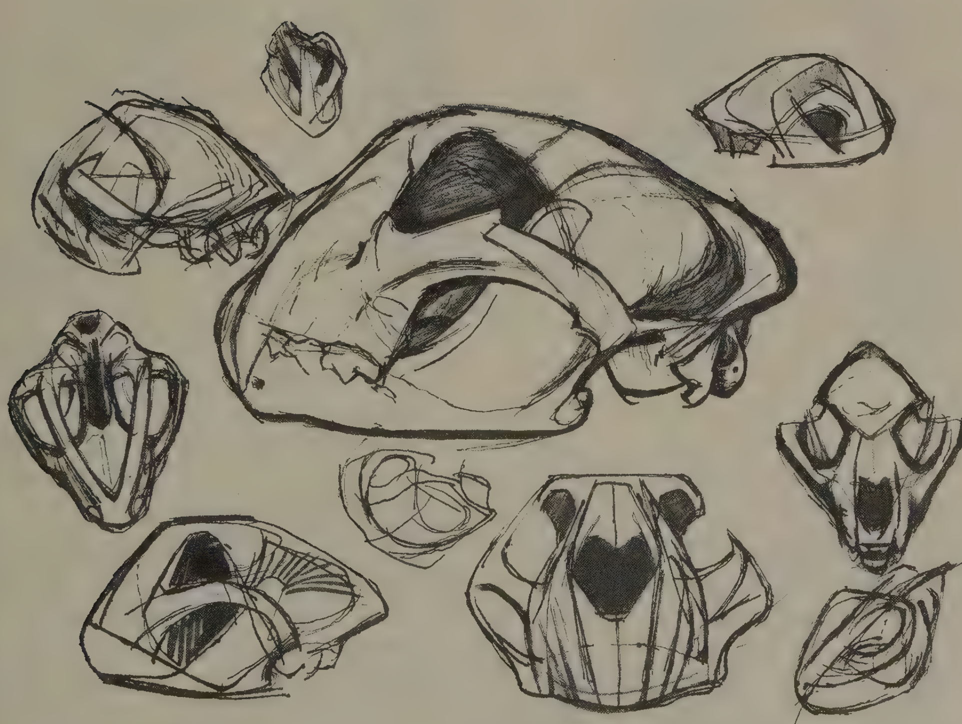
Wild hybrids are unknown but lioness—leopard crosses have been bred in zoos and lion—tiger hybrids are not always sterile, which emphasizes that the close physical resemblances are matched in the genetic make-up of the big cats.

It is possible that lions, tigers, jaguars and leopards arose from a common ancestor. Since their coat patterns as well as those of some rarer species of leopard can all be derived from rosettes, an early form of leopard seems a likely candidate. This cat in turn might have derived from a still smaller ancestor and there are, indeed, a variety of cats in Asia, the cougar in North America and the golden cat in Africa to suggest an early radiation of medium-sized and sometimes spotted cats. I agree with Ewer's suggestion that the caracal and the golden cat are probably more closely related than the former

is to the northern lynxes and I envisage the two species of golden cats, the cougar, the caracal and some smaller Asiatic species as the remnants of an early radiation. None may be fully representative of their common ancestor but, if the forests were their original home, the golden cat might conveniently exemplify the stock from which the big cats evolved.

Conscious of our own origins from Miocene apes, I have described in earlier volumes the adaptation of forest fauna to life in the savannas as one of the grand evolutionary dramas. If Ewer's proposal that the modern felines might have derived from unobtrusive and smaller ancestors is correct and if these were primarily forest animals then the big cats have played star parts in the drama.

A raison d'être for this work has been to assert that the true magnitude of our own emergence as men can only be imagined in an evolutionary and ecological perspective. It is this that gives a special cultural and aesthetic as well as scientific value to the one regional fauna that still offers us a sample of great mammalian radiations. It is in this perspective that the golden cat, the leopard, the lion can be viewed as the living representatives of an evolutionary progression that parallels our own historic march out of the forest.



Wild Cat (Felis sylvestris)

Family Felidae
Order Carnivora
Local names
Paka mwitu (Kiswahili), Ekisuzi (Lunyoro), Mbaki (Luganda), Nyau (Kikuyu), Gruchikithaka (Kimeru), Ekienzi (Rutoro), Kibordo (Lukonjo), Nyachimburu (Kijita), Saudu (Kisambaa, Kizigua), Kageregere (Kuamba), Kimaro (Lubwizi), Enzangu (Runyankole), Bakita (Lugbara), Entuuru (Rukiga), Olembe (Kinyiha), Ogwang burra (Lwo), Buzib kerti (kalenjin), Lugaho (Luragoli), Shitarongo (Tiriki)

Measurements
head and body
55 (47—66) cm
tail
34 (20—38) cm
weight
5 (3·7—6·5) kg males
4·3 (3—5·5) kg females

Wild Cat (Felis sylvestris)

Race

Felis sylvestris libyca

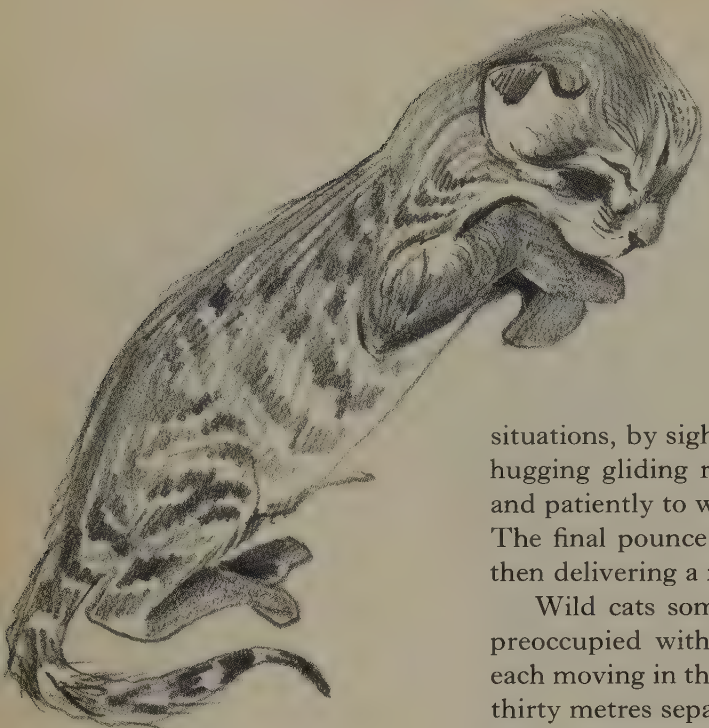
Wild cats are very widely distributed over Africa and Eurasia, while their domesticated descendants are now found wherever man has settled. Amongst the numerous domestic breeds there may be types that have originated from Oriental ancestors but the majority are probably descended from the African wild cat which was domesticated and revered by the ancient Egyptians at least four thousand years ago. Zeuner (1963) has traced the subsequent diffusion of these domesticated cats and there can be little doubt that infusions of local wild strains have been continuous since then. Didier (1949) found that domestic cats in Europe have a baculum that has more resemblance with that of the local wild cat, *F. s. sylvestris*, than with the African, *F. s. libyca*, which suggests that the crossing between wild and domestic cats which still occurs in the more remote parts of Europe was sufficiently widespread in the past to have modified at least this part of their anatomy.

In contemporary Africa, crossings between tame and wild cats are very common. Wild females have been hand-reared and have bred repeatedly with wild forms without deserting their familiar home, where they behave remarkably like domestic tabbies except, as Smithers (1968c) points out they are much more intolerant of other cats; ultimately one animal always drives its siblings, mate or offspring away.

Wild cats are grey or buff with warmer colouring on the face, behind the ears and on the belly. Dark lines and blotches bar the body, limbs and tails, while black or near-black fur often occurs on the soles of the feet. There is a distinct correlation between colour and climate, with pale forms living in the drier zones and darker ones in the more humid areas. Many races have been described but nomenclature is complicated by individual variation and also admixture with domestic cats. Pocock (1951) found no difference between the skulls of wild cats from Africa and Eurasia but he noted that the former tended to be grizzled and striped and the latter were spotted or blotched.

Wild cats live in almost all habitats, but they are particularly noticeable in the more open bushland, both in rocky hills and on the plains and apparently manage to survive in waterless areas during droughts. As nocturnal and cautious hunters they are less easily seen in denser habitats, but they are also common in savanna and along the margins of swamps and forests. The principal attraction of such habitats is probably the rats and mice which make up the bulk of their diet. Other small animals (up to the size of a dik-dik) are taken. Frogs and reptiles, including snakes, are eaten and various insects and other invertebrates, solpugids, termites, grasshoppers, spiders, scorpions and centipedes have also been recorded.

The cats hunt by traversing known hunting grounds slowly and silently, apparently being alerted to the presence of prey by hearing or, in more open



Newborn *F.S. libyca*

situations, by sight. Once the prey is located, it is approached by a ground-hugging gliding run, after which the cat inches itself forward very slowly and patiently to within striking distance, which is usually less than a metre. The final pounce depends on the cat's sinking its claws into the prey and then delivering a neck bite.

Wild cats sometimes hunt in pairs or as a family group, each entirely preoccupied with listening, stalking, pouncing and then walking on, but each moving in the same general direction, with distances between three and thirty metres separating them. It is possible that there is some advantage in that prey flushed by one cat is more easily caught by another but, in general, hunting is probably best conducted alone and the predominantly solitary habits of wild cats are clearly adaptive. It is unlikely that companions would normally share food but mothers carry food back to their young. In Europe, *F. s. sylvestris*, have been reported to cache food in the winter but this behaviour has not been recorded in Africa.

Animals can frequently be seen sitting or lying on some elevated but inconspicuous spot. Leyhausen (1965a) has pointed out that it is very rare for cats to come upon one another unexpectedly and that, if they do, a clash may result. He often saw a farm cat sit watching another from some distance and only some time after would it use the same path. This "look-out" behaviour probably derives from the wild cats' system for avoiding friction in overlap areas. Judging from the different frequency of sightings in various habitats, the spacing of individuals is subject to considerable variation. In northern Europe, males of *F. s. sylvestris* have been found to have home ranges of 60—70 hectares, wherein each male regularly uses paths that connect its favourite resting places and trees with clawed trunks or urine marks (Leuw, 1957). Lindemann (1955) usually found uncovered droppings of *F. s. sylvestris* near a spot where prey had been captured and he concluded that both dung and urine have a territorial marking function. Male ranges probably overlap those of females and, judging from tame free-ranging pets, the females are even less tolerant of other cats than males. Although they do not seem to scratch-mark or deposit urine in the ritualized manner of the males, they still drive away other cats from their home or core-area, particularly other females and, while they have kittens, toms as well. Male *F. s. sylvestris* have been recorded actually killing kittens. However, a female probably evades contact with other cats within the more peripheral parts of her range, whereas the male actively defends his area against other adult males (Leuw, 1957).

The female's antisocial disposition is transformed by her oestrus, at which time she repeatedly utters short want cries, rubs her head, rolls incessantly and becomes restless and hyperactive. The signals are soon picked up by a male and it is only during the brief period of her oestrus that a female accepts the close company of a male (and it would seem the only time he seeks it).

Wild cats are probably susceptible to all the diseases afflicting domestic ones. Pythons have been recorded taking them but, once they are mature, predation is probably fairly light even from humans. In fact, wild cats are frequently attracted by rats and insects to the close vicinity of villages, where they are sometimes killed by dogs or are trapped and shot in retaliation for taking chickens but are otherwise ignored.

The wide superstition about killing cats might have very ancient roots, for these animals became the object of a passionate cult in ancient Egypt. The Roman Diorodus witnessed one of his countrymen lynched by a crowd for accidentally killing a cat. Herodotus described Egyptians neglecting the fire to rescue cats from a burning house and he witnessed the gigantic annual

carnivals that were held in Bubastis, or "the house of Bast", where cats were sacred to the goddess of pleasure, Bast. This was originally a lioness goddess personifying the sun and fertility. To please Bast (who provided protection against disease and evil spirits) devotees put bronze sculptures of cats in sanctuaries and carefully mummified the bodies of cats in such hundreds of thousands that they have since been used as fertilizer. Morrison-Scott (1952) examined 187 skulls from an excavation at Gizeh and thought they agreed with *F. s. libyca*. Ancient Egyptian paintings represent animals indistinguishable from the contemporary African wild cats.

When an outsider marvelled that mere cats should cause the people to rally in their thousands around these incarnations of their protective goddess and when Diorodus complained that neither the Pharaoh's magistrates nor the universal fear of imperial Rome could save a man who had killed a cat from the people's wrath, it was saying very little about cats but a lot about the needs of people.

Breeding may take place throughout the year but Smithers (1968c, 1971) noted birth peaks during the warm wet months in southern and central Africa, and Fairall (1968) suggests December—February in southern Africa. In Kenya, Loveridge (1936) recorded two newborn in early March and a half grown kitten at the end of February. I have seen a mother with half grown young in April and a new kitten in West Uganda during December. There may, therefore, be a widespread tendency for the young to be born in the wet season. This is the period when rodent populations are building up and cover is abundant, both factors that would favour the mother and growing young. The onset of the dry season some months later marks the termination of breeding in most rodent species. The "rodent season" might therefore provide the principal advantage for timed breeding and where the overall ecological conditions would merit it, the short gestation period (56—60) days and rapid maturation of the young (independent at five months) would allow individuals to breed twice a year. This has been recorded in Europe where both *F. s. sylvestris* and domestic cats advertise their mating season with much caterwauling; female cats in this region have two oestrus peaks (one in January—February and one in May—June (Matthews, 1941). In the equatorial zone two peaks in the rains and in some rodent populations might also encourage biannual breeding in wild cats but no data is available at present.

The kittens are born in a hollow tree, hole, rock crevice or under heavy cover in dense grass. Litters average three but have numbered up to five. Born blind, they open their eyes at ten days to a fortnight, are mobile and active at one month and accompany the mother hunting before they are three months old. Families of *F. s. sylvestris* move their quarters close to favourite hunting grounds at this time and the period of practice and learning is particularly intense in this species, as the family breaks up before the young cats are six months old. By the time they are one year old they are fully grown and they become sexually mature shortly afterwards. Survival rates of young cats have not been estimated. They live up to fifteen years in captivity.

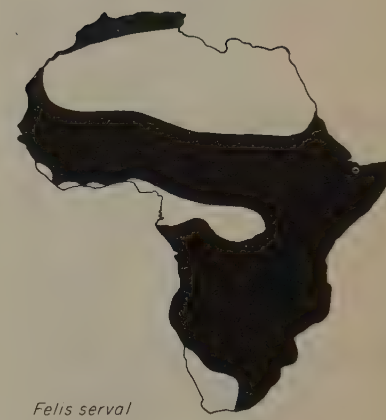
Serval Cat (Felis serval)

Family Felidae
Order Carnivora
Local names
Mondo (Kiswahili), Emmondo (Luganda and many other languages), Monzo (Kirabai), Engalirao (Lukonjo), Orumberembere (Lugbara), Munjuli (Kinyiha), Indama mweli (Luhya), Lutuku (Lugisu), Kurrbalit (Sebei), Kworo (Lwo), Bisdinaad (Somali)

Measurements
head and body
67—100 cm
height
54—62 cm
tail
24—35 cm
weight
13 (10—18) kg males
11 (8·7—12·5) kg females

Serval Cat
(Felis serval)

Servals have relatively the longest legs of all cats, an adaptation that is not for fast running, as is often asserted, but which seems to be primarily related to the problem of hunting small or medium prey in tall grass. Scent-oriented predators can follow the trails of small animals but the serval, like other cats, depends on sight and hearing to detect prey. The former sense is severely impeded in tall grass so the serval is left with hearing, which is very acute and finds expression in the enormous ears. To get an accurate "fix" by means of sound alone the detector needs to gain elevation and this is likely to be the prime reason for the serval's tallness. The long limbs assist spectacular vertical jumps and lightning jabs with the forepaws, but increased striking range is itself dependent on the elevation of the predator's vantage point.



Felis serval

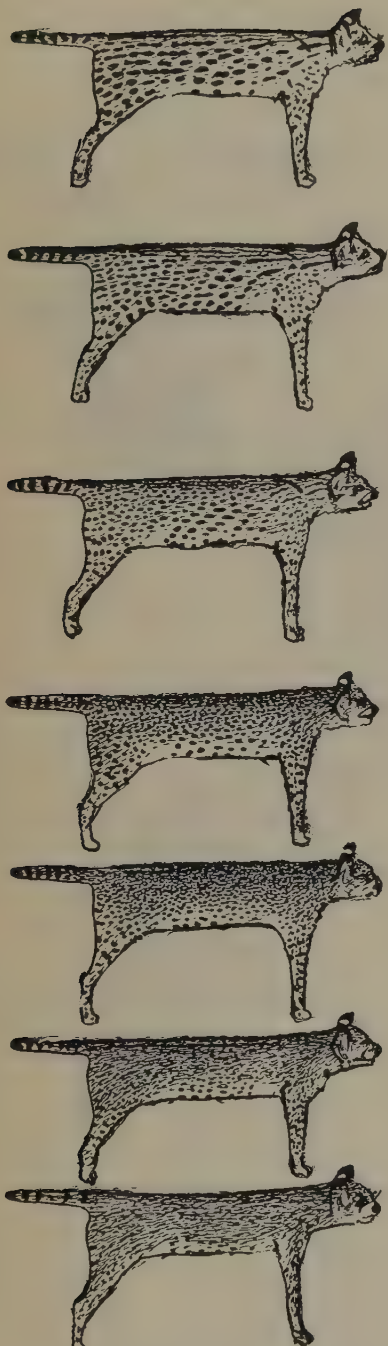
The servals' ears are their most prominent and highly characteristic features. Their backs, like those of the lion and leopard, are decorated with white blobs surrounded by black margins. The ears' role in signalling, however, is evidently subsidiary to their primary function as sound funnels and they are not flickered about in the way a caracal's ears are.

In the more westerly part of the equatorial zone the serval cat's pattern is dimorphic; a fine freckled form (servaline) and a bold black-spotted form occur in about equal ratios in south-western Uganda and in eastern Zaire, a region in which it is common to find both morphs in a single litter. In drier areas further south and east, large-spotted morphs are the dominant or exclusive type. Melanistic servals are common in the highland areas of Kenya and Ethiopia and have also been recorded from northern Tanzania, Tsavo, South Ankole and Karamoja.

Like those of leopards and cheetahs, the serval's spots are probably the product of a process of amalgamation, which suggests that the "servaline" freckle pattern represents a phylogenetically older type of organization. At one time freckled skins were mistakenly assigned to distinct species, *F. brachyura* and *F. servalina*. The predominance of the bold spotted morph in south-eastern Africa suggests that there has been stronger selection for this type in the drier grasslands than in the moister equatorial regions. What this selective pressure might be is difficult to imagine but there is some correlation between humidity and tonal effect (Gloger's rule) in that melanistic servals and servalines, which are darker in overall tone, come from moister areas. Studying servals in the Aberdare National Park, York (1973) described animals with varying degrees of melanism as well as all-black animals.

Servals are found in all the grass savannas of Africa and are common in subalpine habitats including bamboo and forest as long as they are well interspersed with grassy glades or moorland. At lower altitudes, they are abundant along the margins of forest galleries and of reedbeds and marshes. They have adapted well to the cultivation fallow mosaic that is now widespread over the moister parts of Africa.

A very wide range of small mammals, birds, reptiles and insects (notably termites and grasshoppers) have been recorded in their diet but they may, at



F. serval skins (After Weigel)

times, partly abandon predaceous habits. Verschuren (1958) found that four out of seven stomachs of Garamba servals contained mainly vegetable matter and Rahm and Christiaensen (1963) noted bananas and avocado. My own captives sometimes ate quantities of green grass but this is common in many felid and canid species. Judging by published records, hares and rodents are the commonest foods with murid species such as *Mastomys*, *Arvicanthis*, *Lemniscomys* and *Dasymys*, mole rats, *Tachyoryctes* and *Cryptomys*, ground squirrels, *Xerus erythropus* and cane rats, *Thryonomys*, all recorded. Both diurnal and nocturnal prey species are represented and this accords with the observed activity of servals, which is mainly crepuscular and nocturnal but extends into the day in some localities during the wet season; where human settlement is intensive it is generally wholly nocturnal.

Most prey is killed on the ground but a serval has been reported pursuing a hyrax up a tree. Nonetheless, it is not normally arboreal. Verheyen (1951) reported servals killing duikers and the young of larger species of antelopes, such as oribi and bushbuck but Rahm noted that adult duikers are only successfully hunted when there are two servals, and general observations of single cats in fruitless pursuit of small antelopes gives some credence to this.

The largest recorded prey is a female impala on which two servals were seen one early morning; as the animal was killed in long grass she had presumably been ambushed. When prey is fairly large or likely to bite back, the serval springs high and strikes hard with all four feet and delivers a deep and accurate bite. It is interesting that this technique which appears to be adapted to small prey is not greatly modified for larger victims, and York (1973) describes a serval circling for a few seconds and repeating its high spring and bite when it was dislodged by the violence of a baby gazelle's struggles. This 7 kg fawn was only killed after several minutes of effort.

Prey that is first identified by sight is stalked by eye to as close as possible, the cat crouching low on the ground, perhaps raising its head cautiously if the prey disappears from sight. A short rush may follow but chases are seldom sustained for more than a few tens of metres. Birds are sprung upon with a prodigious leap or in a short charge, grabbed with the claws and instantly immobilized with a bite in the neck. Rahm and Christiaensen saw servals excavating *Tachyoryctes* by scratching away their earth mounds and digging into the short burrow. Then they have been seen to leap up in the air and alight on the mole rat. The blesmol, *Cryptomys*, on the other hand, has a very long burrow but hastens to repair the break if an entrance is unplugged; in this case Verheyen reported the serval scratching mounds away and awaiting the arrival of the blesmol which it then seized in its teeth.

I have often watched servals hunting very small prey that was totally hidden in grass, in which case the cats listened very intently and then hooked down at the rustling. If contact is not made with the first jab, the serval continues with a very fast succession of bouncing strikes with neck erect, chin in chest and tail vertical. This is a searching technique for which the long loose digits and their strongly curved claws are particularly well adapted. If the prey is hooked it may be tossed up and then pounced upon or the cat may hold the rat down while it bites the back of its neck and then lets go, watching it intently. When my hand-reared female discovered small *Typhlops* snakes she would kill them with repeated strokes of her paw but very seldom

mouthed or ate them, although this was seen on one occasion. Rustling in leaf litter or in short or flattened grass always precipitates an attack and one must be careful with pet servals not to let one's fingers fidget beneath cover at ground level or the results will be very painful.

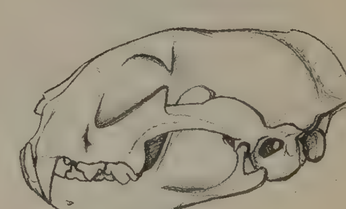
Even when the serval is hungry it may choose to play with the dead or dying animal, seizing it in the mouth and tossing it into the air and often standing on the hindlegs to swipe at it as it falls. This is particularly noticeable whenever the prey is a bird. Servals are accomplished pluckers which suggests that birds are a regular item of their diet. Quails, *Coturnix*, spurfowl,

Pternistes, guineafowls, *Numidia*, and bustards, Otidae have been recorded in their diet. My own captives ate a variety of species and especially relished doves but always refused duck. The plucking technique is also applied but with less thoroughness to hares and it is interesting to see that when birds or hares are lifted in the mouth and tossed, the tossing movements often change imperceptibly into deliberate plucking. In fact the two activities may be homologous, for plucking is unlike any form of chewing, biting or tearing and requires a different type of motor pattern. As playing with maimed or dead prey is universal among felids whereas skilful plucking is not, it is possible that servals and caracals developed their plucking expertize by the elaboration of an innate action pattern. Even captives reared in isolation display the capacity to pluck, so it is not a learned skill.

De La Fuente (1970) mentions servals eating fish and my own captives relished them and would hook live fish out of a basin one after the other with fast jabs of one foreleg and a deft scoop of the wrist which sent the fish flying.

When the prey animal is too large to be eaten at one sitting the serval may cache it. I watched my captive female hide the back part of a hare she had half eaten by scratching leaves, dead grass and other detritus over it with both front and back paws. The same female would sometimes make kicking or raking movements in the litter when she was given a particularly large or heavy piece of meat or, at times, when she had been approached suddenly and silently and therefore appeared to be surprised or nervous.

When this animal was fed at a time when a strange male serval was newly housed nearby, she carried her meat continuously for fifteen minutes, pacing up and down her run with her eyes staring and with jerky movements. Finally the meat was eaten without play in the most secluded corner of her run.



F. serval

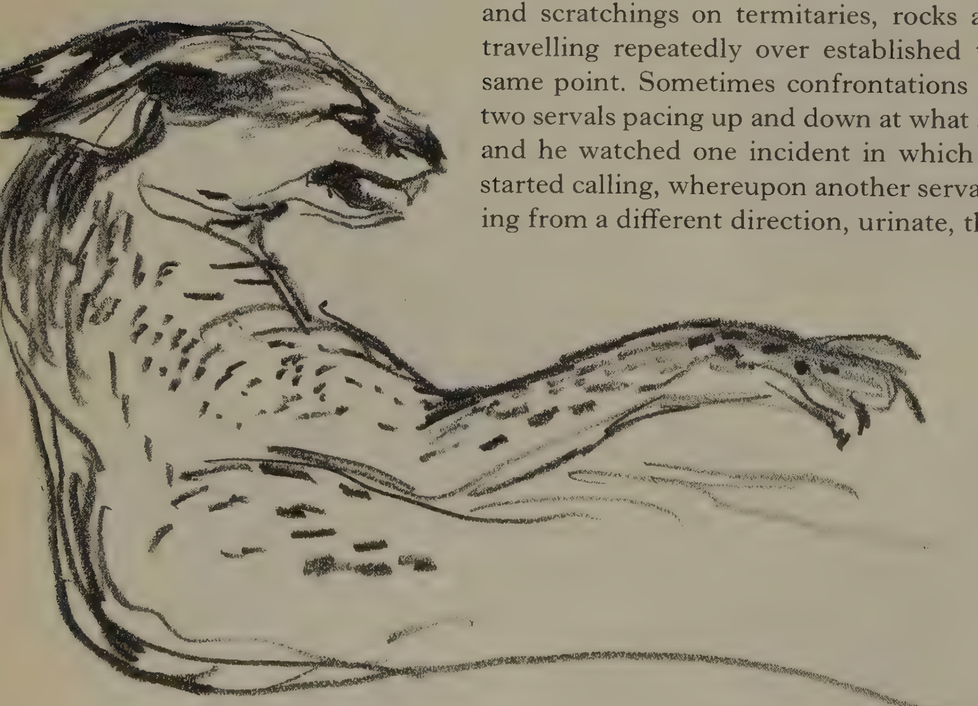

attention
directed
down

The smaller felids seldom share their spoils, so it is all the more intriguing to consider the status of those servals seen sharing or participating in a single large kill. From observation of captives it seems very unlikely that adult females would ever associate and females only tolerate a male during oestrus, an association that does not last for very long and tends to be preoccupied with sexual activity. Juveniles or a mother and her young are not as well equipped to tackle larger prey as adult males, which are appreciably heavier, stronger and more powerfully built.

The extension of tall grass growth that is brought on by the rains must alter the serval's pattern of land tenure and the extension of suitable cover presumably increases the potential range of individuals considerably. Rodent populations generally increase during the rains but are more dispersed. The extension of long grass areas, however, would undoubtedly render large prey more vulnerable to the serval and there is a greater likelihood of antelopes blundering into an ambush. Such circumstances could offer an incentive to servals, also there could be advantages for servals to form associations which could be better able to handle larger prey.

It is thought that there may be a latent sexual cycle in male domestic cats which corresponds to that of the female (Aronson and Cooper, 1966). In the case of the serval cat there is some evidence from Uganda of biannual phasing of the female cycle which is timed to coincide with the two driest times of the year. This suggests that the Uganda servals mate while their ideal habitat is most restricted and their range most fragmented.

It would be very interesting to learn whether males are any more or less tolerant of one another during the wet season when they may be relatively free of a sexual and perhaps territorial role, and whether neighbouring males ever form hunting partnerships during the rains. In Kenya, York (1973) found evidence for territories in the form of urine squirts, dung deposits and scratchings on termitaries, rocks and trees. He described individuals travelling repeatedly over established tracks and routinely turning at the same point. Sometimes confrontations were suggested by the footprints of two servals pacing up and down at what appeared to be a territorial boundary and he watched one incident in which a serval approached a clearing and started calling, whereupon another serval, a male, was seen to enter the clearing from a different direction, urinate, then scratch at the foot of a low bush.



When the animal that had been calling appeared, this male arched its back with its tail up and made threatening calls. The other cat responded to the threats for half a minute but with lowered fore-quarters and when the male approached it moved off with frequent backward glances and growls. The male sniffed the spot where the departee had stood and after scratching the ground defaecated and then followed the retreating cat. It is interesting that captive serval cats exhibit a sexual difference in their defaecating habits, females using the same place while males drop their dung in an apparently more random way. The habitual spraying of particular posts by male servals leaves a greasy and powerfully scented deposit and when repeated several times causes green growth to wilt, thus increasing the conspicuousness of the mark.

The postures of servals are very exaggerated. In aggressive encounters the ears form a flat plate with a characteristic curl to their decorated tips. With heightened intensity the back is arched and the serval stands on greatly elongated legs in a laterally presented stance. The dorsal fur bristles, the eyes blaze and ferocious explosive barks and growls are interspersed with long-reaching slashes of the forepaws. If one cat approaches another with the body half crouched and tense this indicates a readiness to flee. The head may be raised and lowered on the long neck several times before there is a further advance and the eyes remain wide open, the ears pricked and alert.

A curious swallowed mew seems to signify friendly recognition and may be followed by an abrupt about turn and a shiver-display of the vertical tail, which is the most conspicuous signal in the serval's repertory.

A female betrays the onset of her oestrus by a very short, sharp miaow which has considerable carrying power and is repeated in bouts. When approached by a male she may purr and raise her chin as she rubs the side of her mouth and cheeks against him or on intervening wire. When my solitary female was in oestrus, she would rub the sides of her cheeks against my knee, hand or face and salivate copiously out of the corners of her mouth, so that one became quite wet with spit. She also lathered herself with saliva but actually used her long tongue while self-grooming. She would stand with her snowy-white chin raised and then bring it down with a rolling, rubbing movement that smeared saliva up her cheek and on to her head and ears. This downward rub was sometimes correlated with dropping on to her chest but with the hindquarters still raised; this approximates to the submissive posture with which a female solicits a male. More commonly the female stands and after rubbing the cheek and neck walks on, leaning heavily against the male, a human substitute, an intervening wire or an inanimate object. As soon as the rump is reached, the vertical tail shivers and vibrates, whereupon she lies down or else turns round very sharply to repeat the performance, purring loudly all the while. When a captive female is in oestrus and on her own, she intersperses bouts of yowling with interminable pacing and frequent but sparing urine squirting at particular points. The vertical tail is always vibrated when this is done and she may smell or even rub her head on the same spot or may lie and roll displaying thereby the almost incandescent white of her spotted belly in the typical felid submission posture. She may rake her claws down a particular tree trunk. My female used different posts for squirting and raking, but both activities are much more common in males.

squinting

The observation of a dominant male raking over a spot that had been scented by an intruder betrays the aggressive symbolism of raking and I have occasionally noticed captives turn round after seizing proffered food and rake the ground with both fore and back legs, a reaction that was generally associated with uncertainty or traces of hostility at my own approach.

Because solitary animals avoid sharing their food, unfinished meals might elicit displaced aggression so that even the act of raking vegetation over left-overs might have originated in aggressive "no-sharing" impulses.

Like other cats servals may lie up on an eminence, such as a termitary, usually during the morning, where they can sunbathe for a while before retiring to a concealed retreat. I have found lying up spots under flattened reeds or tall grass and suspect that servals may keep circulating, for forms do not show signs of lengthy occupation.

The young are reported to be born in a well-hidden retreat in dense vegetation, in a hollow tree or down a hole, and Verheyen (1951) suggested that they leave the shelter earlier than most cats.

Gestation lasts 64—78 days and eight records of births from Uganda and eastern Zaire suggest two birth periods during the wet season, one in March—April and the other between September and November. This accords well with data from the oestrous periods exhibited by captive females, which reach their peak in the dry periods of December—January and between June and August.

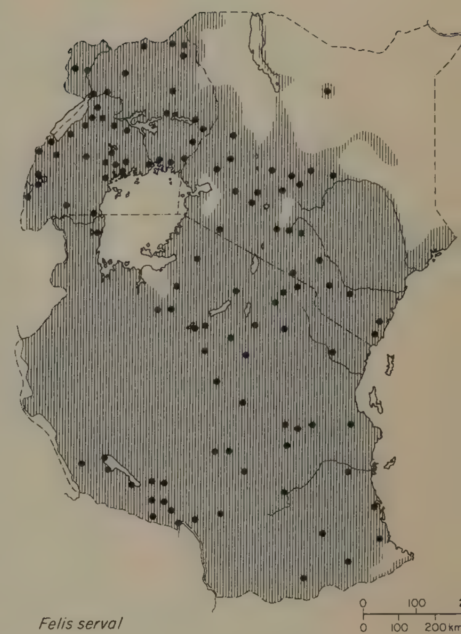
Two or three young (range one to five) are born, blind and helpless; their tail is short and their ears relatively short and folded (see drawing) but the growth of the ears is astonishingly rapid.

The young attempt to accompany the mother at about three weeks but a captive mother has been seen to keep returning her young to the nest whenever they tried to wander (Boston, personal communication). Up to about three months old they make a curious chirping noise. If left on their own they hide and freeze at any disturbance and remain absolutely still although following every movement with the eyes. If reared from infancy they can become handsome pets and are a favourite zoo animal. They will breed in captivity and can live to at least thirteen years.

They are probably subject to most feline diseases and a male I kept died after several days of intense irritation of the skin, during which he literally plucked out all his hair. It may have been co-incidental but the condition began two days after having received a bite from an adult *Cricetomys gambianus* that he killed and ate.

Leopards have been seen to pursue servals and dogs not infrequently bring them to bay by driving them up a tree, although it is apparently not unknown for a serval to kill a dog.

The skin of this species is sometimes sold as a "young leopard" or cheetah and commands a good price in the local skin trade; as a result this cat is no longer found in heavily populated areas.



Felis serval

Caracal
(Felis caracal)

Family Felidae
Order Carnivora
Local names
Simbamangu (Kiswahili), Esakanuli lowale (Karamajong), Anywe (Langi), Mwai (Lwo), Gthuthaney (Somali)

Measurements
head and body
76 (60—91·5) cm
height
38—50 cm
tail
23—31 cm
weight
14·5—19 kg males (females average about 1·5 kg less)

Caracal (Felis caracal)

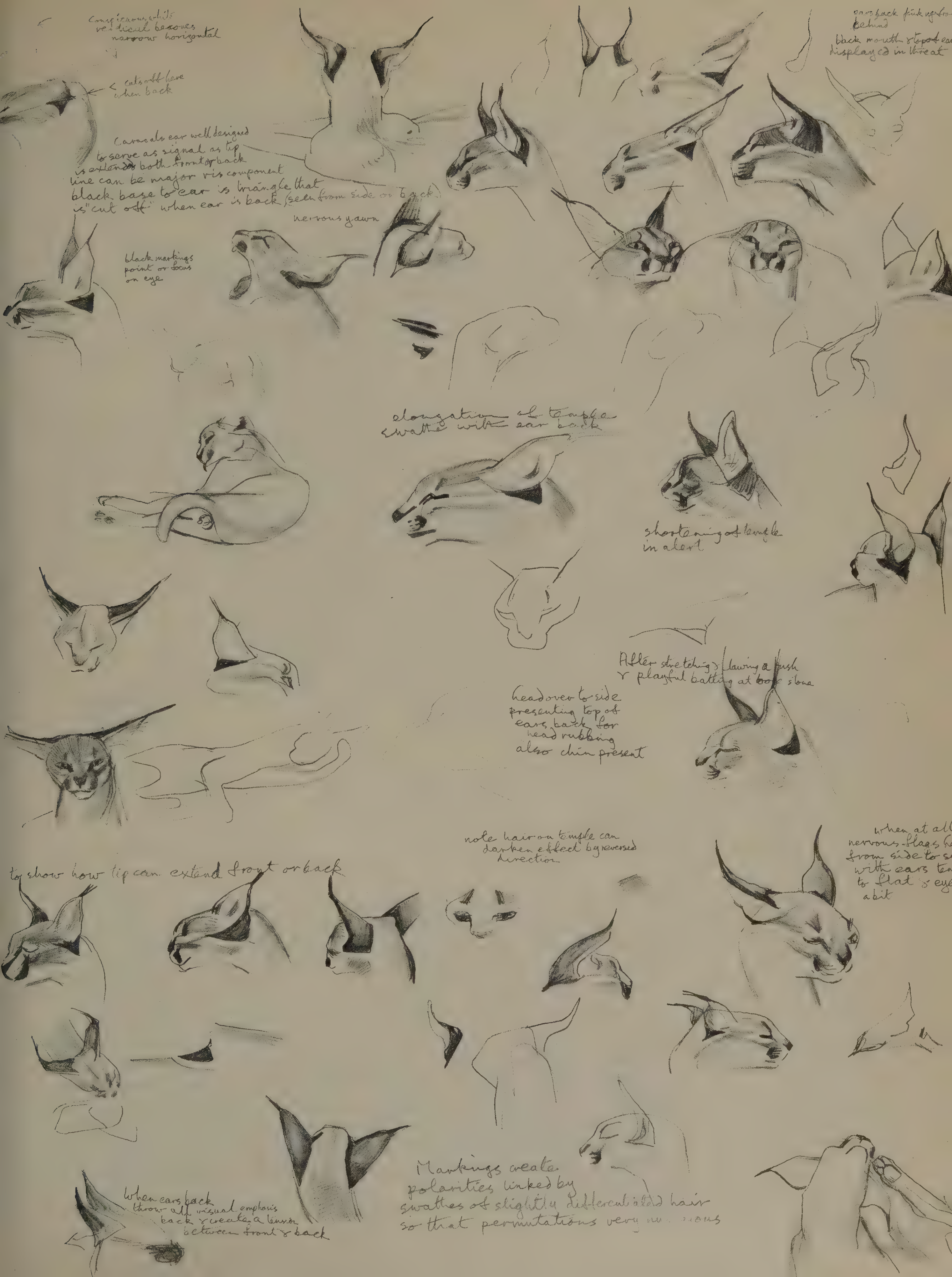
The caracal is a slender rather tall cat of sandy colouring which may be greyish or reddish fawn. On the belly and inner sides of the limbs there are irregular spots and blotches which are generally faint but may be quite distinct in some individuals. The broad handsome head is somewhat snub-nosed and has a smaller muzzle than the golden cat, with which it has a general resemblance in size and proportions. However the most striking features of all are the ears, which are not simply devices to enhance hearing but have become important vehicles for expression. All cats communicate with their ears but the caracal's ears have evolved into a highly mobile and extraordinarily decorative signalling structure. In spite of making an otherwise well camouflaged predator more conspicuous in its relatively open habitat, intra-specific social needs would seem to have prevailed. The ears are lined with long white hairs within but are black behind and, although this colour is sometimes modified by grey flecking, both the rims of the ear and their bases have crisp black margins which serve to isolate the ears visually, making them stand out from their background like a black butterfly settled on the palm of one's hand. In fact, several felid species, including the golden cat, have similar colouring but none possess such large ears nor is the design as highly geometric and precisely defined as it is in the caracal. The long tufts on the tips serve to emphasize the linear direction of the ear; whether this tuft extends the line of the inner or outer edge depends on the position of the ear, and of the viewer. In some old individuals the tips droop in an arc. Although the tufts decorate or elongate the ears in a striking manner, the contrast of black and white can be suppressed in a direct frontal view by being slightly flattened and pulled back. This is the position when the cat is stalking prey and a narrow wedge of sandy fur along the leading edge of each ear helps to reduce the conspicuousness of these organs. From directly behind the ears, generally, have the appearance of two black triangles but they are sufficiently flexible for the conch to be directed backwards, in which position the hind margins pull in towards the centre line; while this may enhance the animal's ability to detect sounds coming from behind, its visual effect is to display two white wedges with heavy black borders (see drawing). This position of the ears is generally associated with slight tension and consciousness of another animal's presence behind. However, for the most striking contrasts of black and white to catch the eye, a cat must turn its head to one side or the other and in this the caracal appears to be peculiarly obliging even to human observers, turning its head from side to side and flickering the ears. All cat species appear to respond in similar ways to casual encounters with members of their own species. They sit down—or sit up, as the case may be—and look at one another. At this stage each animal tends to look away quite often. In the caracal, this turning from side to side could be called head flagging with some justification, as it appears to be more frequent and more highly ritualized than in other species and it is associated with various emphatic but often very rapid movements of the ears. The

commonest outcome of such encounters is for each cat to pass on its separate way. No field study has been made on the caracal but one might assume that the ears help to determine the outcome of such encounters by conveying information as to the status and intentions of each individual. As with many carnivores, erect ears tend to express alertness and confidence while retracted ears imply a defensive or nervous state. Likewise yawning is associated with situations of mild conflict and this gesture is a vivid display of the teeth against the black lips and their white furry surrounding edge. The black and white contrasts around the mouth and on the ears represent two poles on the head with the eyes in between.

In common with several other members of the cat family, caracals have often been described in anthropomorphic terms as having an "arrogant", "lazy" or "haughty" expression. In the case of the caracal this appellation may be encouraged by the eye being very effectively masked by the fur of the upper eyelid. This is particularly noticeable in strong daylight and may represent a protective adaptation against the sun's rays and glare in a desert dwelling species. The eye only opens widely when the animal is very alert, tense, or at the height of threat, therefore the eyes become prominent at close quarters in situations of some excitement. The longer-range visual effect is for the overshadowed eyes to become linear links between the ears and muzzle (see drawing). When the ear is cupped forward into its most alert position, the area of the temple is greatly contracted and the tip of the ear may overhang the face.

In common with other long-eared carnivores, fur on the caracal's temple is adapted to the continual contraction and expansion of the skin beneath by being sparser or more vertically implanted. Each ear is given a linear base by a wedge of intense black fur which surrounds the back of the ear conch and follows round the lower margin, so that black is visible even in side view. Contrasting strongly with the white of the ear's inner lining, this triangle of black changes its configuration with every movement of the ear and from the back it serves to emphasize the ears as units distinct from the rest of the head.

Former range of Caracal



Conspicuous white vertical becomes narrow horizontal
< cuts off here when back
ears back pink up front behind
black mouth & striped ear displayed in threat
Caracals ear well designed to serve as signal as tip is extended both front or back
line can be major vis component
black base to ear is triangle that is "cut off" when ear is back (seen from side or back)
nervous yawn
black markings point or focus on eye
elongation of temple swathe with ear back
shortening of temple in alert
After stretching, clawing a bush & playful batting at stone
head over to side presenting top of ears back for head rubbing
also chin present
note hair on temple can darken effect by reversed direction
to show how tip can extend front or back
when at all nervous flags head from side to side with ears tending to flat & eyes ... a bit
When ears back throw all visual emphasis back & create a tension between front & back
Markings create polarities linked by swathes of slightly differentiated hair so that permutations very numerous

Numerous races have been described, mostly on the basis of small differences in colour or tone, features that are known to vary. They are known from Turkmenia and the Karakorum desert in Russia (where Sapozhenkov (1962) has described their ecology), through Afghanistan and the drier parts

Felis caracal

of India to Syria and the Arabian peninsula. In Africa the caracal is well distributed around the margins of the Sahara and is common in all Somali habitats and in the Kalahari desert. Between these two arid areas the caracal is scattered in pockets of drier country across central and eastern Africa.

There is a short wet season and minimal grass cover in the caracal's habitat; the cat is equally at home on plains or in rocky hills and will live in *Acacia* and *Commiphora* woodland or thicket country. It has often been observed trotting along paths at dusk or after night-fall with a long fast lope and it is likely that an individual hunts over an extensive area. The recorded diet includes numerous small mammals and the young of some larger ungulates; the list includes dik-dik, duiker, hyraxes, hares, various rodents and monkeys, some of which have been seen being killed during the day. The caracal is, however, primarily nocturnal and feathers leave evidence that

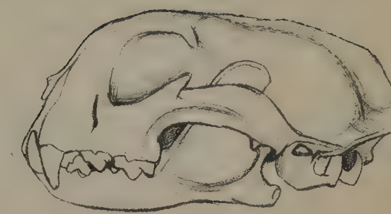
perhaps its most important food is birds, which are for the most part caught while they sleep. Arid or semi-arid steppes and bushland support a variety of francolins, guinea-fowls, pigeons and bustards that are successful and common species, yet the caracal will tackle larger birds as well and there are records of a sitting ostrich and two species of eagle, tawny and martial, killed while roosting at night. Direct observations of caracal's hunting are scarce and have generally been made during the day or of captives. De La Fuente (1970) records them stalking and batting down sand-grouse at a waterhole and I have found the feathers of numerous pigeons and a brown parrot killed by a caracal at a small waterhole in a rocky river-bed, apparently during the middle of the day. The cat is capable of killing more than one bird at a time, but in this instance drought had ensured that there was an almost continuous stream of birds coming to drink; the cat plucked the birds in the immediate

vicinity of the water, although Roberts has described them taking prey up into the forks of trees. The caracal may be the origin of the English expression of "putting a cat among the pigeons", as this was apparently a sport in feudal India with wagers laid on which captive caracal could knock down the greatest number of birds at one rush.

The caracal can make very fast dashes, which Vigne (1842) described as quicker in proportion than those of the cheetah; it is an agile climber and a great leaper. Alan Root, who has kept this species for many years, has seen springs from a crouched position of over two metres high; one of his animals performed for the photographer Dominis, who illustrated beautifully how a bird could be hooked and pulled to the mouth in one deft flying movement (Dominis and Edey, 1968). When small mammals are killed the action is also very fast, the prey being hooked into and seized at the nape of the neck. On these occasions the caracal approaches its prey to the nearest concealment and may then wait for a long period before making a very fast dash, after which it usually carries its prey back to cover immediately. Azzaroli and Simonetta (1966) saw a caracal release a dik-dik which kicked out vigorously.

Like the serval cat, this animal may sometimes eat vegetable matter and Bothma (1965) has recorded a substantial amount of grapes in the stomach of one killed in South Africa.

Animals normally hunt alone but pairs come together for mating. The young only learn to hunt and to fend for themselves after following their mother for some months. De La Fuente (1970) states that they are territorial and notes that they urinate on suitable landmarks such as grass tufts, rocks or tree bases. The feline vocabulary of miaows, growls and spitting hisses is present and loud coughing calls have been heard during the mating season (Fuchs, personal communication).



F. caracal

On the basis of some captivity and wild records in Kenya, Cade (1968) stated that caracals bred between November and May. Under the different climate of the Kruger Park in South Africa kittens have been seen in the same period. In zoos there may be two litters in quick succession, as little as three months apart, but this is most unlikely to occur in the wild.

Gestation is 69—78 days and three (1 to 6) young are born in some secure shelter, a cave, a hollow tree or down an aardvark's burrow. Gowda (1967) has described the courtship, birth and rearing of captives in some detail. The young open their eyes at 10 days, start eating solid food at the age of about two months and are weaned at any time between the 10th and 25th week of life. They can reach sexual maturity between six months and two years.

Like other lesser felids, this species has been the victim of lions (Pienaar, 1969) and its young may be vulnerable to several other predators. However its principal limitations derive from the availability of food and perhaps from the amount and type of cover in its habitat, for it gives way to the serval cat in all areas where grass is widespread for a large part of the year.

Caracals were portrayed in wall paintings by the Ancient Egyptians and

embalmed bodies have been found as well. They modelled these animals in valuable bronze or gilded the sculptures of these and other cats, elegant hieratic figures sitting upright and positioned as guardians of the tombs (see below). In India and Persia they were occasionally trained to be released after pigeons and small game. The Karamajong greatly admire the cats' ears and liken their tufts to the feathers worn for dancing. Although this species occasionally kills lambs or kids, it comes into little conflict with the pastoral people who dominate its habitat and there is no evidence of any noticeable decline in its numbers. The fur is of no commercial value. Captives have lived up to 17 years.

Golden Cat (Felis aurata)

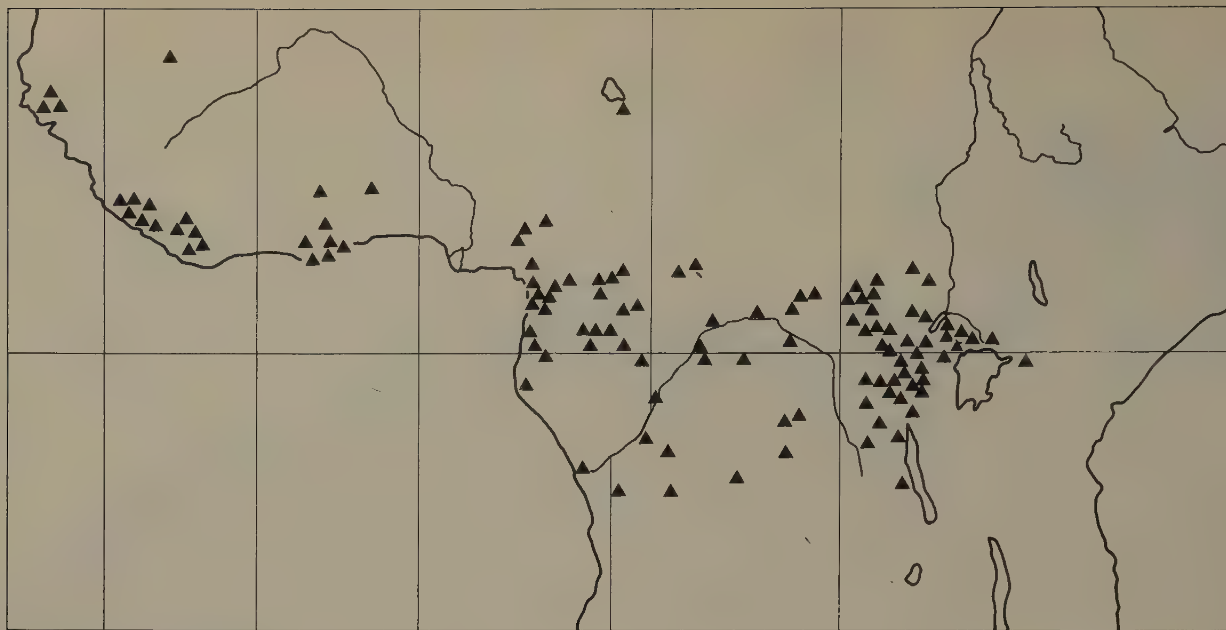
Family Felidae
Order Carnivora
Local names
Embaka (Lukiga), Ekinyange (Lukonjo), Semaguruet (Kipsigi)

Measurements
head and body
61·6—101·6 cm
height
38—51 cm
tail
16—46 cm
weight
5·3—16 kg (very few records).
Males larger than females

Golden Cat
Felis aurata

Felis aurata is a powerful cat with a heavy muzzle and rather small black-backed ears. As with other cats males are considerably heavier and more stoutly built than females, particularly in the head and neck. Adult sizes are rather variable as is the proportion of the tail.

The pattern is subject to even greater variation than that of *Felis serval*, with some West African specimens approaching the common serval in the intensity of their large spots or rosettes, although the background colour varies from shades of red or yellow to smoky grey. Weigel (1961) suggested that the pattern of African golden cats might follow a transcontinental cline, as there is a distinct bias towards the back and legs being plain in the east, whereas spotted forms are more frequent in the west. Whilst all golden cats



Distribution records for *Felis aurata*

Geographical distribution of skin pattern in *Felis aurata* (after Van Mensch and Van Bree)

	Senegal	Sierra Leone Liberia	Ghana	E. Nigeria Gabon Cameroon	Zaire (Congo) basin	E. Zaire E. Africa
Bold, overall spotting	0	60	12	2	0	0
Finer, fainter spotting	0	7	0	18	4	0
Spotting on limbs and flanks only	0	1	0	6	9	15
Unspotted (except ventral surface)	3	0	0	9	3	26

have bold black blotches on a white or off-white belly and are similarly blotched on the inside of their legs, individuals can be found in which spotting is either absent (2nd and 4th row, left), is very fine or faint and limited to the shoulders, lower legs and flanks (3rd row, left), forms a more extensive flecking of the limbs and flanks or covers the entire body (2nd, 3rd, 4th rows, right). Like the leopard and the serval, the size of the spots appears to be graded. Very fine flecks can be free (1st row, right) or clustered into larger spots (4th row, right). These in turn may be regrouped into still larger spots (1st row, left; 3rd row, right). Incomplete marking tends to be correlated with the smaller spots, while the large blotched types always have their bodies completely covered in pattern. Nonetheless, some individuals are entirely covered in very fine flecks (1st row, right).

Although skins of *Felis aurata* are relatively rare in collections, Van Mensch and Van Bree (1969) were able to examine a total of 175 pelts from various localities across the continent and classified them by degree of

spotting. They discovered that the completely spotted forms were commonest in the Guinea Forest Refuge (particularly in Liberia), and they recorded patternless individuals from the extreme west, Senegal, as well as the east; two intermediate grades were widely distributed and the entire range of morphs turn up in the Cameroon—Gaboon area. This distribution of morphs can be interpreted in at least two ways. Either the populations in the Central and Guinea Refuges represent two differentiated populations with a "hybrid" zone between them or the golden cat is by nature a highly polymorphic species, the outlying populations of which have reduced genetic potential and so show less variation. Van Mensch and Van Bree recognized two races, a spotted form, *Felis aurata celidogaster*, west of the Cross River and a plainer form, *F. a. aurata*, east of the river Congo (Zaire), a taxonomic arrangement which implies an original separation of populations. This may prove to be correct, but until there is a more precise understanding of the mechanisms involved in the variation of felids it seems better not to attempt any subdivision of this species. Melanistic and semi-melanistic specimens are known (see A in colour plate).

When the first specimens of this cat found their way into the hands of taxonomists, their very varied colouring gave rise to a plethora of names, but as early as 1883 Elliot noticed that a grey specimen had a reddish tail and he suggested that there might be seasonal changes. At the turn of the century a captive in the London zoo was observed to change its coat colour entirely, rufous being transformed to grey in a matter of four months (Pocock, 1970a), and Brooks (1962) mentions grey young turning red with age. It is certain that differences in colouring are not directly linked with either age or season, as captives of both types have grown through many seasons without changing their colour. Dekeyser (1945) suggests that hormonal secretions may influence coat colour, once again there is no direct link here with sex as both males and females can be red or grey, but it is possible that the observed colour changes in individual cats could be related to internal biochemical changes that have a socio-sexual significance. Changes of colour are not due to patchy moulting but would seem to be caused by an overall fading or brightening but the mechanism for this change is completely unknown. The underfur of all golden cats is grey and the red colouring is due to the presence of a red pigment in a short middle zone of each hair, while grey hair is simply depigmented.

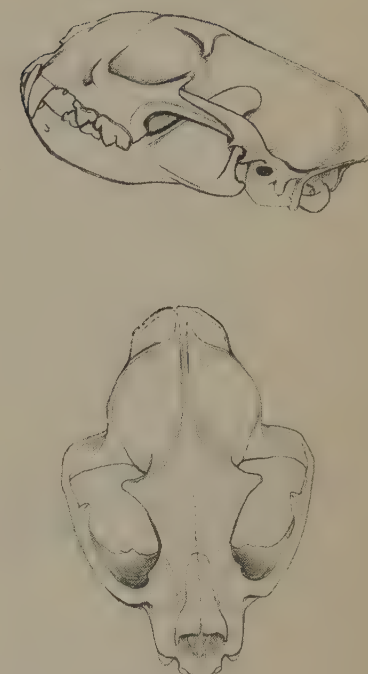
It is hard to believe that colour is entirely without significance for the species, particularly when one remembers that the closely related Asiatic golden cat, *Felis temmincki*, appears to be consistently red. Yet, throughout the African forest belt golden cats are as often grey as they are red and sexed specimens show an equal division of colour between males and females. Although the range of pattern variation is apparently not very great in eastern Africa, combination with colour allows a wide range of possibilities. The colour plate illustrates a variety of morphs from different parts of Africa. The map opposite shows the overall distribution in Africa and the relative frequency of plain, spotted and intermediate cats in six longitudinally divided regions.

As can be seen from the map, most records are from the forest zone, but golden cats have been found in outlying areas, in secondary vegetation and

along riverine strips. They are also common at high altitudes in several mountainous areas where they live in the alpine moorland, sub-alpine and bamboo and montane forest zones.

Golden cats on Ruwenzori live mainly on rats, *Otomys* and *Dasymys*, hyraxes, *Dendrohyrax arboreus*, and red duikers, *Cephalophus nigrifrons*, and the great abundance of these prey species probably explains why golden cats are particularly common in that area. The leopard also shares the same habitat and food supply both on Ruwenzori and in virtually all other parts of the golden cat's range. In spite of their overlapping ranges and considerable similarities in diet and habitat, the golden cat generally feeds on smaller prey and seems to be particularly characteristic of areas with very dense, moist secondary undergrowth. In the Bwindi Forest Reserve there are extensive areas that were heavily felled in recent years by pitsawyers. The destruction of the canopy has encouraged very dense undergrowth, which in turn shelters large numbers of rodents, duikers and monkeys. Leopards were common in this locality before the felling but have virtually disappeared since. Golden cats, on the other hand, are now conspicuously successful and not infrequently attack duikers caught in snares set by the local Batwa and Bakiga. Examination of dung revealed the remains of duikers, monkeys, rodents and birds. Elsewhere in Uganda golden cats are locally common in parts of Bunyoro, Mubende, Buganda and Busoga. These localities are in regions with much forest and dense secondary growth along the valley bottoms which seem to provide a good habitat for the golden cat. Now that human population is

expanding again and reclaiming these habitats, golden cats are commonly caught raiding the hencoops or killing goats and sheep, and cat skins from these areas are sometimes offered for sale. In Uganda, Brooks (1962) described this species inhabiting glades and open forest and he singled out rodents as their food, as does Basilio (1962) who adds gallinaceous birds. The latter author found this species had a preference for river banks in Guinea where he says it hunts on the ground or on the lower branches of trees. In western Uganda, Sugiyama (personal communication) saw a golden cat chasing close on the heels of a red duiker, *Cephalophus callipygus*, in daylight. Other observers have seen golden cats active and hunting during the day. Brown (personal communication) saw one during the afternoon resting on the bough of an exposed tree in a heavily logged and overgrown area, and I have seen two animals sunbathing and grooming one another on a disused pitsawyers' platform at about 9 a.m.



F. aurata

They are said to stalk and rush their prey and captives will attempt to stalk small birds, moving in a rapid low glide with frozen pauses. Gallinaceous birds such as guinea-fowls and francolins would need to be actively stalked on the ground during daytime or grabbed from the trees during the night. Captives hook into their prey and get in a rapid bite at the back of the neck. The Asiatic golden cat, *F. temmincki*, is an able jumper and Gee (1961) describes a tame captive leaping two metres into the air to catch a thrown ball which it would chase and retrieve for hours. When taken for walks, this animal would rapidly dash up almost to the top of a tree, down again and then repeat the performance at the next tree. This apparently playful behaviour suggests that the cat's hunting may depend upon exceptional alertness and dash both on the ground and in trees. The African species is also known to be an able and active climber. There is no evidence of it adopting the leopard's strategy of awaiting prey.

These cats have good senses of smell, hearing and sight and in spite of having been observed about during the day they are also nocturnal. Their large greenish eyes are evidently able to function under very dark conditions in the forest undergrowth. Small ear pinnae are not necessarily an indication of poor hearing and in the case of *F. aurata* the bullae are large and the external ears may be more of an adaptation to the overgrown nature of their habitat, for very thorny plants such as *Acanthus* and *Calamus* could be a hazard for large delicate ears. The common cat-like sounds, hissing, snarling, growling and miaowing have been heard in captives.

I have found the dung of golden cats on pathways without any sign of associated scraping or scratching. Blonk (1965) and Rosevear (1974) postulate that this may signify adaptation to arboreal life.

Individuals are normally solitary, but two very red cats I saw together in Bwindi Forest were probably adult in spite of a noticeable difference in size. Nothing is known about this species' social life or behaviour, nor is it known how large an area they range over. There are, however, small localities, often near paths or tracks where foresters have reported seeing them from time to time which could imply some regularity of habits.

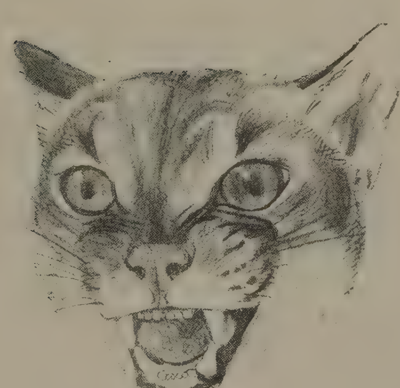
I have not found descriptions of the young nor records of breeding dates. A few young have been reared from infancy and both species of golden cats are apparently docile and make much appreciated pets if hand-reared. Wild

ones instead are well known for their ferocity if trapped or captured and do not tame; Durrell (1954) described a caged one leaping up and striking through the bars of its cage at his face.

A heavily pregnant female was trapped in south-western Uganda in early September 1971, her head and body measured only 70 cm and her eviscerated body weighed 5·5 kg illustrating the relatively small size at which females may be sexually mature.

Judging from the lack of published information these cats would seem to be extraordinarily discreet about where they conceal their young and Rosevear (1974) suggested that the lack of records might imply arboreal sites for their litters. Caves and other rocky crevices have been reported to provide them with shelter and one might presume that the young are also born and hidden in such retreats wherever the terrain is suitable.

Although they are probably less rare than is generally thought, attempts to study animals in the wild are made very difficult by the density of their habitat and the near impossibility of seeing these cats before being detected by them. Even observation of captives could reveal a lot more about them than is recorded at present and their colour and polymorphism should be susceptible to interesting experiments. Captive golden cats have been recorded as living 17 years but this may refer to the Asiatic species. A recent review and list of literature on this species is contained in Van Mensch and Van Bree (1969).



Leopard (Felis (Panthera) pardus)

Family Felidae
Order Carnivora
Local names

Chui (Kiswahili), Shuwi (Kisambaa), Sui (Kizigua), Subi (Kisukuma), Tsui (Kirabai), Ng'ui (Kinyaturu), Nsui (Kinyaramba), Nzowe (Kinyika), Ngue, Ngwe, Engwe (Kisumbwa, Luhya, Runyankole, Kuamba, Lukonjo), Ęnge (Luganda, Lunyoro, Rutoro), Ngo (Kikamba), Ingo (Kijita), Inge (Kitaita), Ngari (Kikuyu), Rungu, Obasi, Nyamanduu, Rumu, Linganyi (Kichagga), Mbishi (Kipare), Duma (Kihehe), Narocho (Kimeru), Kwach (Lwo), Oluwaru keri (Masai), Lowuoru keri (Samburu), Oduwo (Lugbara), Oro (Madi), Geras (Kiliangulu), Erisa (Ateso), Melildo (Sebei), Chaplanga (Kalenjin), Shabeel (Somali)

Measurements
head and body
104—180 cm
tail
67—110 cm
weight
60 (37—90) kg males
50 (28—60) kg females

Leopard
(Felis (Panthera) pardus)

Races

Felis (Panthera) pardus pardus	Mainland
Felis (Panthera) pardus adersi	Zanzibar

The leopard's spots are a spectacularly beautiful device by means of which it contrives to see and yet remain unseen. It is my own uncertainty that remains vivid in my mind when I remember my first boyhood encounter with a leopard. A hint of movement and the shock of awareness that I was looking into two opalescent eyes—the movement away was so swift it scarcely gave substance to that disembodied stare. Beyond this shock of cognition there is only the memory of an incomplete and fleeting optical impression.

If the leopard is designed to be invisible to prey and enemies alike, its coat pattern and its behaviour are well suited to this end and my childhood experience was only unusual in that I did not, on this occasion, walk by oblivious.

Any animal with disruptive colouring is difficult to see, particularly if it keeps quite still against a suitable background, but in the case of the leopard correlations can be suggested between the animal's behaviour and its coat pattern which deserve examination. Leopards spend a large part of their life resting in leafy vegetation. When undisturbed and in relatively open terrain they remain on the ground for much of the time but trees and other eminences are natural refugees and vantage points. Out of 113 observations Hamilton (1976) saw leopards choose trees or rocks to rest in 99 times and under bushes only 14 times. While those in bushes were more difficult to see, Hamilton has stressed that the animals need to anticipate intruders, prey or enemies as well as to find shelter and shade from the sun. Concealment from mobbing birds and primates may also be an important consideration in a life punctuated by very long rest periods of observant immobility (see Vol. I, pp. 137, 197).

Like other forest animals that live a wandering life without a permanent shelter, the leopard must be inconspicuous while it sleeps as well as while it stalks. To serve crypsis effectively a pattern must have an exact relationship to the average disposition and balance of tones and to the average intensity of contrasts in the animal's immediate setting. The larger the animal the less possible it is for it to imitate a specific background like bark or rock so that the need is for a more generalized camouflage. For this to be effective the animal must still be selective about its resting places. Precision in the choice of a resting place derives from the number of specific needs that the site answers and in the case of the leopard there appear to be two principal factors, shade and elevation: of the two the former is more important. The leopard is essentially a forest animal and even those adapted to semi-arid conditions appear to have a physiological need for shade during the heat of the day. Like most cats they choose elevated sites to survey their surroundings. This might be of advantage for ambushing prey and the habit must certainly

Detail of foliage, branches and sky (from a photograph of a wild leopard in a tree) passed through mechanical screens

I	II
Ethiopia	Ethiopia
III	IV
Trade skin	Ruwenzori
V	VI
Zambia	Somalia
VII	VIII
Cape	Zanzibar
IX	X
Zambia	Mt Elgon

assist in detection of prey and enemies but it is probably of greatest significance in the regulation of contacts between leopards.

These two considerations are manifest in the leopard's choice of trees or, in more arid countries, rock outcrops to rest in. It is significant that Hamilton (1976) found rocky hillsides were less attractive to Tsavo leopards during the wet season and there was a wider use of the range because all the trees were in leaf, giving the animals an enormous choice of suitable shelters. The particular mimesis of the leopard's coat appears to be the dapple of leaves and their shadows but the light and dark areas are actually disposed in an abstract conformation that breaks up the tones into broad averages of area and contrast. For example, the grouping of spots has a remarkable resemblance to ink spot clusters found in colour photographs that have been printed after passing through mechanical screens.

The invasion of habitats outside the forest might be a secondary development which has not greatly affected the original pattern formation. Some sort of rosette pattern was probably already fully developed in the common ancestral stock of leopards, jaguars, lions and tigers: the lion shows almost perfect rosettes in cubhood, while tigers sometimes exhibit a gradation of markings, ranging from lozenge-shaped rosettes to full stripes.

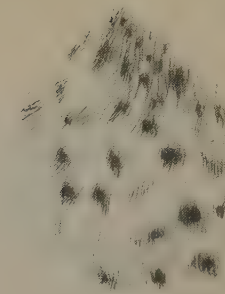
No two leopards have the same pattern and numbers of aberrant individuals have been collected and described. Some of these are illustrated in the colour plate opposite. Individual variation has made it almost impossible to delineate races although coat colour is often correlated with ecological conditions. Thus leopards from the arid Horn of Africa (colour plate, 6) are very pale, while those from the more humid highlands of Ethiopia (2) have a darker ground against which the rosettes have enlarged and become solid black patches. On the Ruwenzoris, leopards are also apt to be darker than their lowland neighbours and there is a local tendency for the margins of the rosettes to be peculiarly geometric (4).

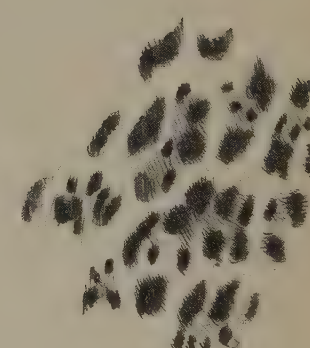
On the basis of what is known generally about pattern formation and by referring to a variety of leopard morphs it is possible to suggest how their beautiful pattern might have evolved.

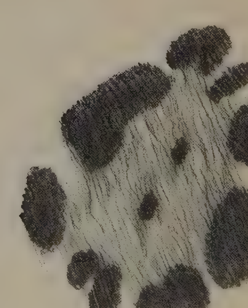
It has already been pointed out that the felids present their vulnerable throat, chin and unprotected underparts in friendly encounters with members of their own species. The signal value of these areas and of the ears and tail tip has encouraged the development there of maximum contrasts of black and white. As with many mammalian species a leopard's individual hairs are coloured in the agouti pattern. It is known that a multiplicity of bolder patterns can emerge from the overall agouti grizzle when the proportions of light, dark and intermediate pigment bars are systematically ordered. While the rosette pattern might ultimately derive from agouti it has become an independent pigmentary system (Robinson, 1969). Contrasts can evolve out of insignificant differences of tone in agouti or in relatively uniform ground colour, selection favouring the progressive intensification of darker and lighter elements. Such a straightforward build-up of tonal extremes is only suited to highly conspicuous signals and in the leopards the black and white underparts are kept well-hidden when the animal is crouched or stalking (see p. 317). Tonal contrasts are modified on other parts of the body by the presence of at least two tones of ground colour in addition to the black

spots. In some aberrant individuals there may be areas of neutral tawny colour densely freckled with minute spots of darker and lighter brown, in others the dark spots are slightly larger and darker but the two tones of ground colour tend to separate out into independent areas. Sometimes there is a tendency for the densely freckled areas to form panels (as in 5), while complexes of black spots tend to be associated with equal areas of the lighter tone; often large areas of freckle are interrupted by uneven patches in which the three tones are strongly separated (as on the hindquarters of 7). Thus the lighter areas appear to be balanced out with, or complemented by, the scattering of small black spots. The true leopard rosette consists of regularly disposed patches of darker colour around which the black spots cluster and graduated examples of this clustering can be seen on the foreleg of the Zanzibar leopard (8).

This example illustrates the basic unit from which the rosette pattern is constructed. It consists of small separate spots disposed around patches of orange. The multiplicity of rosettes in the Zanzibar leopard is linked with the small size of the black spots. The small rosettes can coalesce and form large more boldly defined ones and incomplete amalgamation can sometimes make a very irregular figure. The average number of rosettes is the product of this secondary fusion, which suggests that the Zanzibar leopards are a peculiarly conservative population. Two, three or four lesser rosettes can join up together providing the basis for an infinite variety of rosette shapes and numbers. Figure 10 illustrates a pattern with an average number of rosettes, although the ginger colouring of this Mt Elgon specimen represents the brighter end of the leopard's colour spectrum. These bold secondary rosettes can in turn combine together to form still larger rosettes (9), although such jaguar-like morphs are extremely rare.







Leopard with large rosette pattern (Maisailand) (from a photograph)

Another type of spot amalgam involves the suppression of the intermediate colour and the closing up of the margins of the rosettes to form solid black spots. This occurs in the lower part of the hindlegs in most leopards but extends to the rest of the body in the Ethiopian leopard (2) It would seem that random linking up of this type of bitonal pattern can lead to the extra-ordinary marbling shown in Fig. 3 (see Pocock, 1935). Ansell (1967) pointed out the resemblance of this skin with that of the king cheetah. The similarity is interesting as cheetah patterns are not complicated by a third colour or tone. The aberrant leopard described by Ansell (5), while showing some resemblance with the former, includes "panels" of very fine freckling on the trunk and shoulders, which hints at the type of pattern organization seen in the oriental clouded leopard, *F.* (*P*) *nebulosa*. Ulmer (1941) has described a leopard in which the spots amalgamated to form stripes on the back. (This does not seem to be the process by which tiger stripes originated. They are, instead, greatly elongated rosettes.)

In the amalgamation process that I have hypothesized the progression is in the opposite direction to that envisaged by Weigel (1961), who regarded the basic pattern of the Felidae as a series of dark markings which could break up to form smaller spots or, in the case of the leopards, pale in their centres to produce rosettes. Close observation of the disposition of spots reveals that this is a very unlikely explanation. The three skins on the left (3, 5, 7) may have been the product of a faulty replication of the rosette pattern but it is interesting that they illustrate a tendency for spots to merge into larger units. The fusion of black on the centre-line of the back is noticeable here and black may extend very much further over the body, leaving sometimes only the face, throat, belly and the legs white and tawny with black marbling. Schouteden (1945) illustrates a good example and similar skins have been described from West Nile. As Sclater (1900) and Pocock (1932) stressed, this sort of darkening is entirely different from melanism of the usual kind.

True melanism in the leopard has been defined by Robinson (1969a) as non-agouti and it embraces the entire animal without affecting the rosettes, which show through in reflected light as a more intense black and are spaced in the manner appropriate to the region (Figs 1 and 2). Black leopards, which are often called black panthers, are rarer in Africa than in Asia but they have been recorded on Mt Kenya, on the foothills of the Ruwenzoris and are said to be common in parts of Ethiopia. It is interesting that leopards from humid forests tend to have darker coats and that melanism also seems to occur in similarly humid areas, so that there must be an advantage in being darker in these habitats. The relative rarity of melanism in East Africa may be due to the very small extent of forests, so that continuous infusion of spotted genes from the surrounding populations suppresses the genetic trait.

In captivity, where black leopards have been allowed to breed with spotted ones they have been shown to be an autosomal recessive. Collecting data from zoos, Robinson (1969a) found that black females had consistently smaller litters than normal leopards and he thought that this lower fecundity opposed the unknown advantages apparently possessed by the black morph in certain regions of Asia. The results of his survey of breeding in zoos are reproduced below.

	Offspring observed		Offspring expected	
	Spotted	Black	Spotted	Black
Spotted × spotted	21	10	23	8
Spotted × black	28	24	26	26
Black × black	—	298	—	298

In concluding this discussion of leopard patterns I should mention that leopards have given rise to much taxonomic speculation and repeated re-charting of racial ranges. Any regional population tends to blend with its neighbours so that extensive and ill-defined areas contain leopards with intermediate patterns. Thus the leopard shown on p. 348 from the foot of the Ruwenzoris is something of a blend between the types 4 and 10 shown on my colour plate. I have, therefore, followed Ellerman *et al.* (1953) in regarding all continental African leopards as *F.* (*P.*) *pardus*. As I discussed earlier, the size, number and shape of rosettes is influenced by a process of amalgamation and the variable results include individuals that retain numerous rosettes. None of these approaches the Zanzibar leopard in abundance of spots and I have followed Swynnerton and Hayman (1951) in regarding this island population as a distinct race.

World distribution of Leopard *F(P) pardus*

Swynnerton described leopards as being ubiquitous in suitable localities of Tanganyika, which begged the question of what is suitable. The most obvious requirement is food, but leopards are so adaptable in this respect that they could probably live anywhere in East Africa if this were the only consideration. In the more open habitats they are limited by the presence of other predators and scavengers. Furthermore, it is not uncommon for leopards themselves to become the prey of men, lions and hyaenas as well as competing for the same food supply. A relatively slow pace and lack of stamina limit leopards in their relations with these three major enemies. They depend

therefore upon the presence of trees, broken terrain, thickets and other heavy vegetation both as a refuge and as cover from which they may stalk or waylay their prey. Leopards will use any sort of screen to get within the very short striking distance from which they can launch an attack and in very open country have been seen to use vehicles or even dust-devils thrown up by the wind. Observations of leopards stalking in the open are of course more conspicuous and so are more frequently reported in spite of the habitat's

being somewhat atypical. There is no doubt that leopards prefer to kill in thick cover and that the attack is launched at very close quarters but by the very nature of the action it is seldom seen. The technique for ambushing from an eminence has been observed under conditions in which it was plainly inappropriate. Thus, in very open acacia woodland at Ngaserai, a leopard repeatedly climbed small trees as it followed a herd of gnu. This behaviour made the gnu nervous but in spite of this the leopard eventually managed to leap down on a young one. The need some ungulates have for shade in the dry season may allow a leopard to wait in the branches of a well-used shade tree and then drop down upon its prey, and this too has been observed.

Leopards hunt very largely by sight but sound is important in some circumstances. For example, hunters imitating the bleat of a duiker to attract other duikers very frequently find a leopard comes instead (Wilson, 1966). They have excellent night vision and in some localities they are predominantly nocturnal, which militates against systematic investigation of the full repertoire of their hunting behaviour. Elliot (in Cullen, 1969) was shown a fully grown eland bull that had been killed by a large leopard. By back-tracking, he found that the eland was one of a herd passing along a track in the cedar forest.

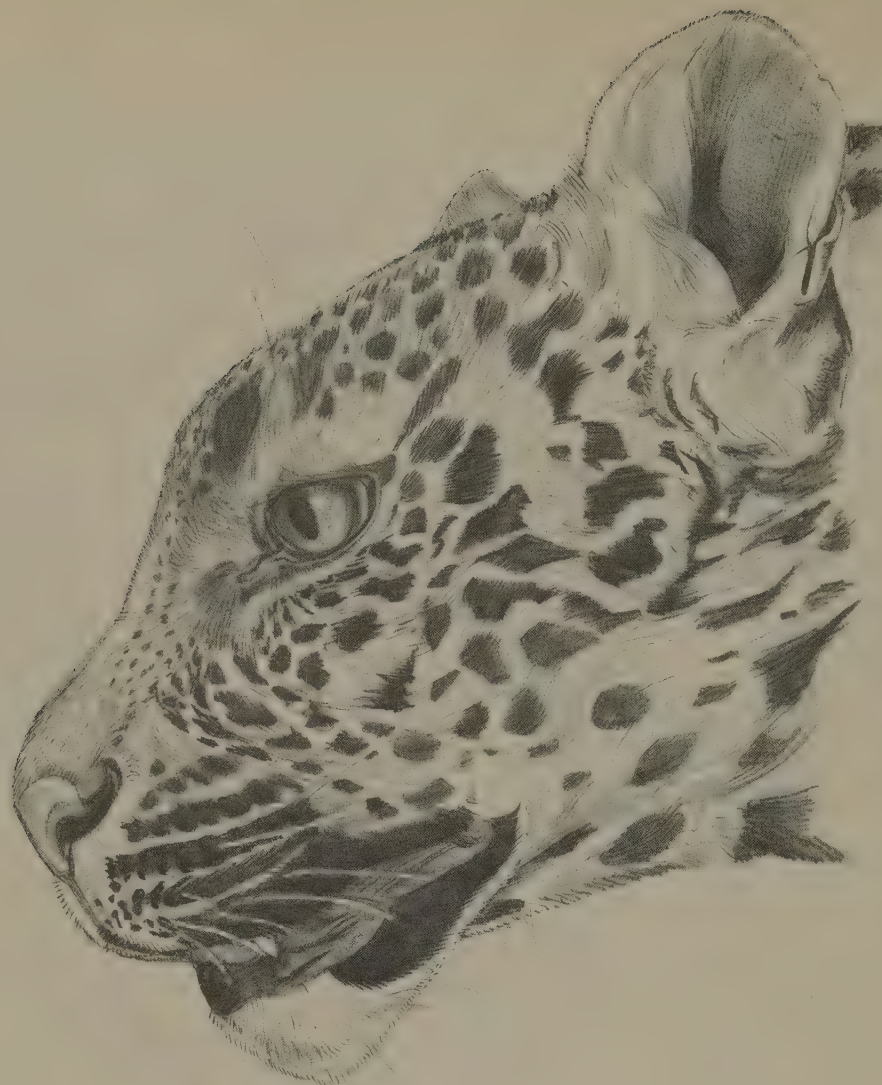
> "The leopard had jumped on to this eland bull from a tree above the track, and the victim had at once dashed downhill. The eland had fallen down twice but managed to get on to its feet again. But on a third occasion the leopard had succeeded in holding the animal down and finally killed it. In the downhill rush and the whole struggle the leopard had lost a lot of hair on trees and bushes. It seemed that the leopard had managed to kill the eland by biting into the windpipe area, and suffocation was thought to be the main cause of death. Damage to the eland's neck vertebrae must have occurred during its repeated falls. While the only teeth marks were in the eland's throat, there were many claw marks on the flank, and it seemed that the leopard had been on top of the eland all the way down. The warden put half the eland carcass in a nearby tree and—on the following evening—spotted the biggest leopard he had ever seen, with its left forehead all bare and bloody. From all the evidence it was certain that this leopard had killed the bull eland without assistance".

In this instance, the size of the prey far exceeded the normal but the incident illustrates what an accomplished killer the leopard can be. On another occasion a female eland was found felled by a leopard within twelve metres of being pounced upon; in this case the claws were imbedded in the neck and the teeth in the nose. A male bushbuck, freshly killed by a leopard and with only a few scratches on the nose and flank, was found to have had its neck broken. It would seem that the hooked embrace and great power of the forelimbs can unbalance prey many times the cat's own size and with the aid of the teeth be applied to the dislocation of the neck or exposure of the vulnerable throat. These incidents may give a misleading idea of the leopard's prey, which generally includes rodents, birds and insects. Although their prey can range from dung beetles or fish to eland, there is a common pattern to the leopard's killing technique, the first action of which consists of a strike with claws extended. This may be a flip, scoop, swat or slamming embrace, the strength and orientation of the movement being graded according to the

size and location of the prey. This is followed by a bite that is generally directed at the neck or back of the head while the paws embrace the body.

Most of their feeding is nocturnal and it would be impossible to measure the success of leopards hunting in undisturbed conditions in a closed habitat. Bertram (1974) has reported only three successful outcomes in 64 daylight attempts to catch prey in the open savanna of Serengeti. In spite of this apparent incompetence, leopards normally have relatively small ranges,

which implies an abundance of food. Hamilton (1976) has noted that they are not greatly affected by a decline in any one prey species and his faecal samples suggested why: 35% contained rodents and 27% birds, 27% small antelopes and 18% arthropods. Hares and hyraxes occurred in 10% and 16% while only 12% included remains of larger antelopes in spite of the area being Tsavo West National Park where there is a relatively high density of antelopes. However, the age and size of a leopard has considerable bearing on the size of its prey. Of the known kills in Hamilton's study area eleven were impala, four bushbuck and three dik-dik. Ungulates are probably only a small part of their diet in the forest. Primates provide a major food item in some forests and perhaps for some individual leopards, particularly if individuals become "specialists" in their own prey choice. I have heard monkeys, baboon and chimpanzees make distress calls or hootings in response to a leopard's coughing at night and I have reported what appears to be mobbing behaviour by monkeys directed against leopards (Vol. I, pp. 197, 224). Remains of monkeys frequently occur in the dung of forest-dwelling leopards, together with the hair of bushpigs, red duikers, bushbuck and even chimpanzees. In the killing of a redtail monkey witnessed by R. White (see Vol. I, p. 227) it is interesting that, after watching the monkeys in an isolated tree, the leopard



should get up into the tree itself, from whence it leapt out to catch a panicking monkey. A similar sequence of events was followed when a photographer set up an elaborately staged performance in South Africa with a captured leopard and a chacma baboon (Dominis and Edey, 1968).

Shortridge (1934) noted that leopards in south-west Africa only attacked baboons at night and especially when they slept among rocks. They are adept at creeping up on sleeping animals and there are records of both humans and their dogs having been killed without waking others in the house; a baby was even taken off the breast of its sleeping mother in this way and roosting hens and guinea fowls are also commonly taken.

A leopard's individual tastes may lead it to ignore easier prey. Estes (personal communication) saw one leopard repeatedly chasing jackals near the Munge cabin in Ngorongoro crater. Another at Busingiro ignored goats completely but took all the dogs it could find. One Kalahari leopard was known to have killed many ostriches—always at night—and this animal ate

the birds' visceral and subcutaneous fat first. Porcupines killed in the same region were never eviscerated nor were the guts eaten (possibly because of the smell of an aromatic bulb eaten by these porcupines).

In the more open savannas the overall diet tends to reflect the prey that is available within or close to the margins of thick cover. In Serengeti the leopards themselves are restricted by competition and habitat; in spite of this, Kruuk and Turner (1967) were able to find evidence of twenty species taken by leopards with gazelles, reedbuck and impala predominant. Around Seronera, territorial male Thomson's gazelles are vulnerable and preferred victims (according to Schaller, 75% of all kills are males) but an abundance of lions and hyaenas ensure that the leopard's hunting forays out of the wooded riverine strips or stony outcrops are short and brief. The importance of their arboreal refuges includes their own safety from lions (which have on several occasions been seen to kill leopards) and immunity from interference because, on the ground, their prey is soon lost to lions, hyaenas, jackals or vultures. Caching food in trees is not entirely determined by competition but the practice is said to be less common in areas where the prey is safe from scavengers; if trees are scarce, as in parts of the Kalahari, leopards have been known to put their prey down an *Orycteropus* hole and scratch soil over it (Fuchs, personal communication).

In rocky areas, boulders may take the place of trees as vantage points and feeding spots. In the Matopos, leopards living in this habitat feed mainly on the dominant small animals, hyraxes, red rock hares, duikers and klipspringers (Wilson, 1969).

In Olduvai Gorge, a pair of leopards were once seen watching klipspringers for about half an hour before both started to stalk moving on parallel courses about fifty yards apart. Working their way to within thirty or forty yards, both leopards made a flat-out dash. Such behaviour is unusual but it illustrates that a basis for social hunting as commonly seen in lions exists even in the solitary leopard.

In the Kruger Park, impalas are the dominant fauna and provide 78% of the leopard's diet and they are killed without any special bias as to age and sex. Other commonly killed species are kudu, warthog, duiker, bushbuck and baboon, which are also more abundant species, but the killing of a disproportionate number of young waterbuck reveals that the lyingup behaviour and the habitat of this species renders this class more vulnerable to leopards. Among the 31 other species recorded from this area are aardvarks, steinbuck, porcupines, bushpigs and many cane rats, hares and guinea fowls (Pienaar, 1969).

Another example of selective hunting is Schaller's report (1972b) of female bohor reedbuck being killed twice as often as males. This author has estimated that a leopard kills on average slightly more than one animal a week, totalling about 1,000—1,200 kg a year; this represents an exceptionally economical rate of predation and is half the prey biomass eaten by a cheetah. The reason for this economy is the habit of caching and returning to feed on prey, even after it is decaying, so that a single carcass can last four or five nights. As for the amount of meat eaten at a single sitting Turnbull-Kemp (1967) estimated a range of 8·1—17·6 kg in twelve hours.

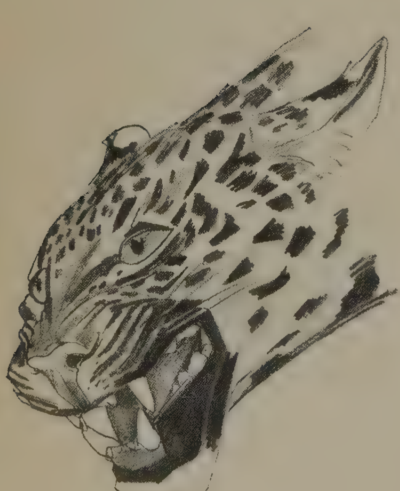
A female with her consort or large young may hunt together for a while

and Verheyen has claimed that the former association results in the killing of larger prey. However, hunting and feeding are normally strictly solitary and exclusive activities and no neighbouring leopards would be tolerated near a kill. Leopards on their tree caches have frequently been seen to interrupt their feeding to pursue a variety of animals that are not their normal prey; these attacks suggest that protection of the carcass may be an important element in their behaviour and leopards have been observed to kill cheetahs, serval cats, genets, spotted hyaenas, a secretary bird and European storks. When such victims are caught they are often hung in a tree and are sometimes eaten as well. It may be this behaviour pattern that initiates habitual killing of one species. Estes (1967) saw a leopard kill eleven jackals in three weeks and in Amboseli a number of hyaenas were killed over a short space of time and hung up in trees. However, there was no evidence of the latter's having been eaten, whereas jackals, like dogs, are common prey. It is possible that a taste in jackals or dogs might begin, or be reinforced by, a prey-protection impulse triggered off by the sight of these smaller carnivores.

Leopards do attack one another over food, and a female that was found dead in Samburu might have been killed in a contest over a food-cache as the two leopards had fought over the remains of an impala. The victims of fights do not seem to be regarded as food items, but a male leopard shot from a hide in the Loita Hills was subsequently carried off by another male visiting the bait. At dawn this leopard was discovered eating the carcass about 150 metres away. In spite of several records of leopards hanging up cheetahs they had killed they do not seem to subject their own species to this treatment. An incident that occurred in south-west Africa resembled the last mentioned report but with a territorial connotation.

> "Late one afternoon I shot a male leopard fairly far away from my ox-cart but eventually put it down to fetch it the following morning. I found the dead leopard terribly lacerated, but not eaten into. I left it on the spot and embedded a trap beside it in which I caught a big male leopard in the following night."
> (J. G. Fuchs (personal communication))

This incident illustrates how fiercely a leopard will attack a trespasser within his area. The heads of leopards are frequently scarred and there are records of several fatal encounters between leopards in the records of the Kenya National Parks. These seem to have been the result of unexpected head-on meetings: two of the victims (a young male in one case, an aged female in the other) were bitten through the skull but in another report death was the result of a swipe of the paw cutting an artery.



Corbett (1956) noted that leopards in India did not tolerate intrusion by strangers of their own species and Hamilton (1976) has recorded a number of fights in Tsavo which suggested accidental encounters and, in one case, a deliberate interception. He pointed out that fights tend to occur only after avoidance mechanisms have failed to prevent an encounter and he was able to plot the movement of ten radio-tagged leopards over a period of three years. He found an enormous variation in the area of leopard home ranges; from nine to sixty-three square kilometres but the animals spend most of their time circulating through about half their total range, walking in the region of twenty-five kilometres in a night and up to seventy-five kilometres when

disturbed (Turnbull-Kemp, 1967). However, a leopard covers a great part of its range every few days and seldom rests in one spot for two nights in succession. Hamilton found that leopards might share as much as 70% of their ranges and the core areas of two Tsavo males were only 0·8 km apart although the average spacing was 2·8 km and the overall density about one leopard to every thirteen square kilometres.

Eisenberg and Kleiman (1972) estimated the minimum range of Ceylonese forest leopards as 8—10·5 sq km. He thought there was little or no overlap between adult males but females might share a part of their range with a male. His observations give added credence to the assertion that trees are raked more along the boundary of a male leopard's territory.

> "It scratches, scrapes ground and sprays urine. Scratching trees are repeatedly visited by the same leopard and one tree in particular appeared to be very near the boundary of two adjacent home ranges. A scratching tree may show a lean or have a very large limb approximately six to eight feet off the ground. When a leopard approaches such a tree it sniffs at the base and then springs rapidly on to the branch or climbs up the sloping trunk. It pauses to sniff at previous scratch marks, extending itself along the branch. Then suddenly tensing its shoulder muscles, it begins scratching with its forepaws, or it may crouch and scratch backwards with its hindfeet. It may spray urine around the base of the tree and impregnate the base with exudates from the paws or from the animal's body as it scratches or reclines on its ventrum. While reclining at full length the leopard may rub its chest or perineal region on the limb or rub its cheeks on points which apparently bear traces of odour."

Home ranges of one female and three male leopards on rocky hills in west Tsavo, Kenya. Textures indicate intensively used or "Core" areas (after Hamilton 1976)

Schaller (1972b) has noted that female leopards squirt urine more than lionesses, a difference that may emphasize the greater importance of indirect communication in leopards. Dense habitats give a special value to acoustic means of communication; the most commonly heard sound is a coughing grunt made by a leopard breaking cover; this may be an alarm or warning cry. Turnbull-Kemp (1967) described a leopard treed by dogs making a loud caterwaul and defensive captives make a typically felid explosive hiss. Captives also purr at one another and Wilhelm (1933) described wild males occasionally announcing their presence with deep purring, which was answered by an approaching female. An abbreviated but louder purr call is made by a female summoning her cubs, which may be answered with very cat-like miaows or whimpers.

Adult leopards sometimes advertise their presence with a peculiar rasping noise that can be imitated by dragging a lungful of air over the constricted glottis. Each burst of sound is regularly spaced from the next and lasts about as long as the rasp of a handsaw cutting a log, to which it is often likened. There are usually about eight rasps in succession but there may be over twenty. If another leopard is within earshot, this sawing call is often answered and the resulting duet presumably conveys information about the caller and enables each to react appropriately. On one occasion, Hamilton (1976) located three radio-tagged leopards in an area where their ranges were known to overlap. Two were males, one of which was accompanying a female. Nine sets of calling were heard in about half an hour and the solitary male turned back into his own home range when he was about one kilometre from the other two. Eisenberg and Lockhart (1972) have reported that in-

dividuals in zoos can be roughly characterized by the number of rasps to each call and they noted that the rate of calling increases during oestrus. They also correlated the movement of two leopards calling and answering each other and found a definite avoidance pattern.

Shortridge (1934) stated that rasping was heard almost nightly during September and October in Okavango in south-west Africa and he believed it was associated with a mating season. Fuchs (personal communication) also noted a peak in rasping and reckoned there was a mating season in south-west Africa, starting about August, and noted a sort of barking howl, which he thought might be associated with mating. Hamilton also heard this call made by a male while it was copulating and delivering ritualized neck bites. Eisenberg and Lockhart (1972) thought there was a peak in sexual activity between August and November in Ceylon. Like yowling in cats and roaring in lions, it is possible that rasping repels neighbours while at the same time assisting contact between a bonded pair. Hamilton (1976) found one female had sporadic contacts with at least four males but when she associated with one individual she accompanied him in his own home range. The fact that pairs associate for only a fairly brief period could explain why calling tends to be persistent when it is heard and why animals are silent for long periods of the year. Should sexual activity follow seasonal rhythms, a peak in such behaviour could be expected. Records of births from East Africa are inadequate at present but those that exist are sufficiently scattered to show that some breeding is going on all the year, although breeding peaks cannot be discounted. Observation of captives has revealed that oestrus lasts from about a week to over a fortnight. If fertilization is not achieved, there may then be an interval of 45·8 (20—50) days (Schaller, 1966). Gestation lasts 92—105 days and three or four (two to six) young are born in a hollow tree, cave or aardvark burrow. Females with very young cubs temporarily abandon their nomadic circuits and keep their young in a single shelter unless severely disturbed. Cubs are blind at birth, measure about 150 mm and weigh 43—60 grammes. The eyes open between the age of six to ten days and they start to eat solid food at about 42 days, at which time they begin to emerge from their shelter and go off milk as they gradually accompany the mother on longer and longer expeditions. They are weaned at three months, by which time they weigh about 2·7 kg but are still dependent on the mother. While

small, they will crouch and freeze in response to the mother's low growl. Play resembles that of other cats with much wrestling and pouncing. Rushes often end in a somersault as the momentum carries the hindquarters over a firmly-embraced play-object or playmate. Captive cubs like to hook into fabrics, particularly curtains or coats, from which they dangle kicking and mouthing. Growth curves for captives have been recorded by Crandall (1964) and it seems that they continue to put on weight over a very long period. For example, a two-year-old weighed only 45 kg. Schaller (1972b) noted that cubs broke their association with the mother at about 22 months but he records a female cub beginning to travel independently of the mother at 13 months.

Bertram (1974) was able to observe a young leopard become progressively more independent. At first the mother fetched the young one and led her to the kill. Once the kill was consumed, both animals parted again and hunted on their own, the youngster with less success and with much more attention to small animals. Only when the mother had mated again did the young one begin to succeed in catching larger prey. Bertram remarked that each animal presumably knew where the other was at any time because of their frequent smelling and urine-marking of tree trunks.

In some areas the independence of the young might initiate a nomadic phase and there have been reports of wandering transients coming to grief when they have raided livestock and even dustbins.

A very lean subadult that was killed scavenging the remains of fish in a fishing village was found to be suffering from numerous cysts in the liver. Johnson (1964) has isolated a herpes type virus from the spleen of a leopard cub. Murray (1967) has recorded bleeding and necrosis in the lungs of Kenya leopards and the symptoms of a common canine complaint known as Nairobi bleeding disease. Sachs (1969) found Diphyllobothriid tapeworms in the intestines and Haffner *et al.* (1969) pentastomids in the nasal sinuses. Pienaar (1969) recorded one death from anthrax in South Africa.

Leopards are quite frequently killed by lions, particularly when they are very young. Schaller (1972b), who has seen such attacks, has remarked that facial expressions, bared teeth and vocalizations are typical of those seen when lions are attacking one another and he suggested that riverine forest in Serengeti may not be the leopard's preferred habitat but more a refuge from the very numerous lions.

Hyaenas also take very young or ailing leopards and Kruuk (1972b) has seen hyaenas appropriate leopard kills; but he also reports a case where the tables were turned. The leopard approached a hyaena that was eating the remains of a cheetah's kill. After a brief struggle the leopard seized the kill and took it up a tree. After eating, the leopard came down and charged the hyaena. Leakey (1969) has reported leopards attacking hyaenas in defence of their young.

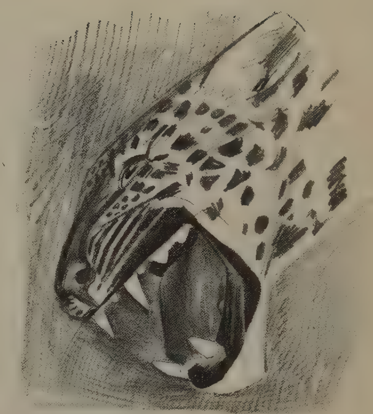
Wild dogs have also been seen to drive a leopard off its kill but it turned and, charging back, seized its prey again and climbed a tree with it.

During daylight, baboons will unite and chase leopards. On several occasions I have called up the large males of a troop to within a few metres by imitating a leopard's sawing. Kortlandt (1967) has filmed chimpanzees belabouring a stuffed leopard put in their pathway.

Various ungulates will defend themselves from leopards and occasionally succeed in killing them. In an interesting record of the death of a leopard from snakebite, Fuchs (personal communication) wrote

> "In 1912 I found in the Belgian Congo a dead leopard about ten months old. From the scratched-up soil beside the carcass I inferred that the animal had died less than an hour ago, after having been lying on the spot for days in the throes of death. His right foreleg was very swollen and beneath the skin I found the three-quarters-of-an-inch-long hollow fang of a viper. The tissues under the skin on the leg and the whole right side of the body were charged with extravasated black blood. This leopard had obviously succumbed to the bite of a large viper."

Whether this was the result of an attempt at killing the snake or an accident due to the leopard's silent soft-footed tread was not clear but Fuchs was told by Hottentots that such casualties had been known to occur also in south-west Africa.



The major limiting factor on leopard populations is undoubtedly people. The commonest source of conflict is, of course, stock raiding but very occasionally leopards can actually become habitual maneaters. At least one attack has been traced to rabies but other instances have been traced to particular individuals that took to eating people, rather as the Ngorongoro leopard took to jackals. Between them two leopards at Kalingombe in Ubena killed twelve children and two adults in 1948. Other maneaters ate seven people in the Njombe area and ten in Chimala during 1951—52. In Kigezi about fifteen people were killed in 1929 by both lions and leopards. All these reports were from areas in which there had been a recent expansion of human population and in the Ubena—Njombe region these events were closely synchronized with even more extensive killings by lions. This illustrates the tendency common to both these carnivores to eat whatever prey is most readily available.

A much more frequent source of human casualties is wounded or trapped leopards. While making their extensive museum collection Roosevelt and Heller (1915) noticed that quite small traps would hold a leopard and that they would often splinter their teeth on them. Pitman (1936) reported a man being mauled after catching a leopard and in another incident one man was killed and two injured by a leopard that was caught in a guineafowl trap that had been set for a porcupine!

At this time the use of gin traps was officially encouraged in Uganda and the trade in leopard skins reached its peak in 1944, in which year permits were issued for 2,388 Uganda skins, which, quite apart from reflecting how popular leopard skins are, was a testimony to the great number of leopards in Uganda and how easily they could be trapped.

Traditionally the ownership of skins was strictly regulated in many regions of East Africa. In Karamoja and Acholi skins are part of the regalia of warriors and in Buganda the skin was the symbol of kingship and only the head of a family was permitted to sit upon this valuable fur. The tip of the tail has a special symbolism in Buganda and this finds expression in a ceremony in which the fur from a leopard's tail is burned and smoked in a pipe. This ritual is a magic incantation to call home a straying wife, child or other relative and with the smoke and the oratory is said a prayer that, just as the tail of a leopard is always restless, so may the wanderer's heart be without rest until it returns (Sempangi, personal communication).

The claws are widely regarded as good fetishes for making business stable. In several parts of Africa the whiskers are chopped up very finely and used as a poison, apparently causing peritonitis.

The symbolism of the leopard is very old and widespread. In West Africa it was the symbol of wisdom and images were frequently carved or cast by the Ife and Benin sculptors. In Ancient Egypt the priests of some later dynasties wore leopard skin vestments as did all representations of the goddess of writing, Sekhanit, and a statue of the Pharaoh Tutankhamun was found in his tomb mounted on the back of a realistically modelled leopard.

Totally uneconomical efforts have been made to breed leopards for the fur industry but they are popular zoo exhibits and thrive in captivity and have been known to live up to twenty-one years.

Lion
(Felis
(Panthera)
leo

Family Felidae
Order Carnivora
Local names
Simba (Kiswahili and many other languages), Shimba (Kitaita, Kisukuma), Tsimba (Kirabai), Siyimba (Kirangi), Nsimba (Kinyiramba, Kisumbwa), Insama (Kinyiha), Ngimba (Kinyaturu), Munyambu (Kikamba), Liduma (Kibena), Ebi (Madi), Kami (Lugbara), Ekichunchu (Runyankole), Empologoma (Luganda), Entale (Runyoro, Rutoro), Itare (Kijita), Nyalupala (Kihehe), Maalo (Kichagga), Ngatia, Muruthi (Kikuyu), Ngetuny (Kimeru, Ateso, Karamojong, Kalenjin), Olugatuny (Masai, Samburu), Njetunyido (Sebei, Elkoni), Sibuor, Labwor, Odyek (Lwo), Nyek (Kiliangulu), Libaah (Somali)

Measurements
head and body
172—250 cm males
158—192 cm females
total length
256—328 cm males
238—274 cm females
height
123 cm males
107 cm females
tail
61—100 cm
weight
172 (150—238) kg males
151 (122—182) kg females

Lion
(Felis (Panthera) leo)

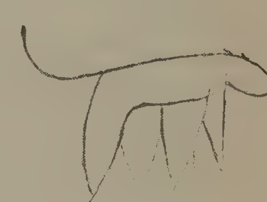
Seen in the context of this book the lion is but the largest in a long series of predators, each of which specializes in catching and eating prey of a type and bulk appropriate to its own hunting and killing skills and to its own size.

Such a detached view is made less realistic by the fact that for centuries lions have been predators of, competitors with and above all a source of symbolism for the human race.

Ranging over a large part of Africa and south-western Asia, the lion has been the dominant large carnivore in these regions for several millennia. Yet this may not always have been so. Among the rock paintings of Cro-Magnon man lions are depicted as well as large felids without manes and without tufted tails. These have been identified with the skeletal remains of a distinct and apparently abundant species, commonly described as the "cave lion" or *Panthera spelaeus*, which inhabited Europe until it became extinct sometime between 340 B.C. and A.D. 100. In the Pleistocene deposits of Africa there are the remains of sabretooths, another large cat, *Panthera crassidens*, leopards and a lion-sized felid with a lower jaw like a tiger—but no lions; which lends weight to the suggestion that the modern lion might be a relatively recent and highly evolved species, its emergence as the dominant large carnivore more or less co-inciding with the rise of man. Our hunting ancestors probably knew the lion a lot more intimately than we do today; yet Palaeolithic men have left remarkably few representations of the big cats on the walls of their caves. When the sinuous silhouette of a lion or lioness does occur, it is immediately recognizable but it is seldom given great prominence.

In Tanzania, the last survivors of the hunting and food-gathering people maintain this ancient indifference and a chance of hunting with the Hadza set off a train of thought which I think illustrates how the borrowing of animal attributes by some human cultures and not by others is linked, in a particularly interesting way, with the structure of the society. The lion provides a vivid analogy between an evolved process and human behaviour (see Vol. I, pp. 110—115). A family of Hadza had ambushed and killed a lion by firing poisoned arrows into it from a hide as it came down to drink. The skin was stripped off and was pegged out without ceremony. I was struck by their indifference to the animal in contrast to urban folk milling around a caged or dead lion, begging the keeper or skinner for lion hairs to win love, lion whiskers to overcome enemies, lion claws for luck, lion heart to become brave—scarcely any part of the body is without its magic. Each of the crowd clamours in the hope of enhancing himself in the eyes of his fellows by appropriating an attribute of the king of beasts—all competing for the borrowed glory!

The outcome of such competition in early civilizations finds expression in the monopoly of the kings of Assyria over hunting lions, in the assumption of the title "Lion of Judah" by the ancient dynasty of Ethiopia and in the pretentious titles of more recent empires and armies.



(Tainet)

Assyrian relief from Temple of Tell Halaf

In Buganda, Speke (1863) described in less than flattering terms the royal strut of the king, which was reported to be traditionally founded on the step of the lion and was intended to be a very majestic representation of the animal's gait. Warriors of several tribes make themselves head-dresses or haloes imitating the lion's mane. In fact the lion crops up in the symbolism of a great many civilizations. It is almost as universally present as the lioness is absent and it has to be admitted that the mane seems to alter human perception of this big yellow cat fundamentally. (For example the ferocious Egyptian goddess Sekhmet was usually represented as a maned lioness or lion-headed woman.)

The male's proud bearing, his thundering roar and perhaps the resemblance between manes and beards has invited a specially appropriate image for martial dominance that has never lost favour with aggressive societies and individuals. The assertiveness of this symbolism in a wide variety of civilizations gives a special fascination to the biological meaning of the male lion's most dramatic secondary sexual characteristic, his mane. It has been suggested that the thick matted mane protects the vulnerable throat and neck of the pugnacious lion, but there is no evidence that the lioness is any less lethal a fighter or less prone to attack than the male. Indeed, females are the more practised killers, catching well over three-quarters of all prey, while the very conspicuousness of the male probably makes him a less effective hunter. There can be little doubt that the principal function of the lion's mane is visual rather than physiological or protective. It serves in the first place to make him look bigger than he is, both broadside and head-on, and in some postures the animal acquires a geometric symmetry that is highly distinctive and unambiguous.

The society of lions, like that of man and other species, offers advantages to the male that can intimidate his conspecifics. Felids generally achieve this by advancing crabwise on extended legs with arched backs and raised tail with all their fur fluffed out. Almost all cats enlarge the frontal aspect of their face with something of a ruff, and the open mouth and blazing eyes of an aggressive cat are surrounded by a halo of fur which is marked by various blotches and spots that serve to enhance expression. This common felid behaviour pattern finds its expression in the "lion strut"; this posture is only assumed by adult males as they meet conspecifics, it is directed mostly towards females but also to subordinate males. In this display the lion raises his body as high as possible on rather stiffly stretched legs and tucking his chin into his chest raises the head vertically over the shoulders while the black-tufted tail arches high in the air over the back. The artificial gait serves to increase the size as does the deliberate presentation of the body in profile. There seems to be little doubt that the evolutionary extension of a facial ruff into a shoulder-covering mane is primarily linked with this lateral display. The "strut" is probably very important in assisting the relatively mobile male lion to impose himself on the relatively stable and matriarchally structured pride, for which see later. Lionesses will reject strangers with great ferocity, and the mane, as the principal distinguishing feature of the male probably serves to intimidate the females and thus allow males to be the principal circulators in populations that might otherwise become static because of the female tendency to stay in the same pride generation after

generation. The evolution of a single, very conspicuous feature in only one sex may be partly linked with an increase of visual range as the lion's ancestors moved into more open habitats. Messages that depend on minor changes of posture or facial expression get lost at greater distances so that the ancestral lions probably found coat patterns and fur-fluffing increasingly inadequate and, as the mane developed, they became obsolete. Thus it is possible that the sleek patternless coat of an adult lion is linked with the presence of a mane.

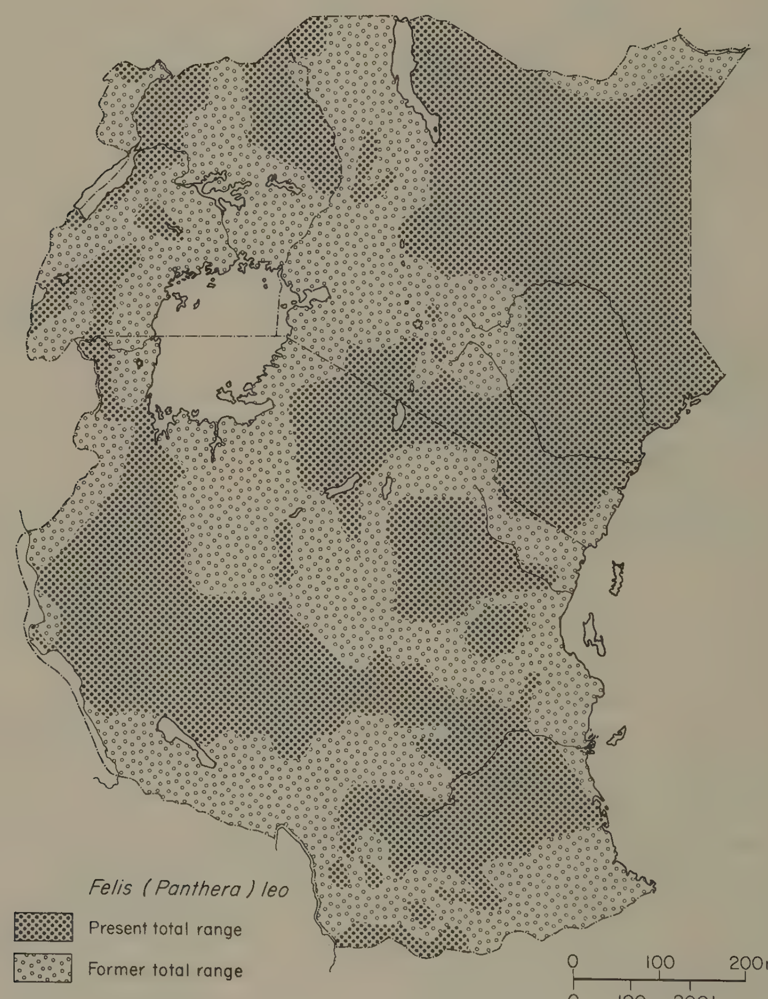
World distribution of the lion in early nineteenth century *F. (P.) leo*

The black colouring of the mane in some lions is not connected with melanism, a phenomenon well known in leopards and many other cats but apparently unknown in lions, although a dark brown animal was once reported from Isphahan in Persia (Layard, 1887).

In cold latitudes lions tend to grow longer and darker coats and in some highland areas of East Africa (i.e. Uasin Gishu) there has been a similar tendency. Occasionally lionesses grow small manes but this is probably due to some hormonal imbalance.

The presence of leopard-like blotches on cubs and on some adults is almost certainly a vestigial pattern suggesting that the lion's ancestors lived in thicker vegetation as most of the spotted cats do. The emergence of the lion as the pre-eminent predator of the savannas, plains and deserts of Africa and Eurasia invites numerous questions. Is the lion's evolution linked with the rise of the gregarious plains' ungulates? Would the exigencies of life in the open encourage solitary cats to become social? Was it the acquisition of a social life that encouraged the differentiation of sexual roles in lions? On the whole recent studies of their natural history suggest affirmative answers to these questions.

The lion was particularly common in East Africa in the very recent past, as it ranged throughout the savannas and sub-deserts of Africa and was present at most altitudes and in all vegetation types except the most extensive forests. Their numbers have been most conspicuous on the open plains but there has always been an obvious correlation between high densities of large prey and lions whatever the vegetation type and its particular spectrum of ungulates. The most famous areas for concentrations of plains animals, Serengeti, the Lake Mburo and Lake Edward flats and the Athi plains, were or still are well known for their large lion populations.



At some time or other, lions will eat almost any available animal, and records exist for a surprising range of prey, from grass mice, lizards, tortoises and quails up to young elephants, bull giraffes, rhinoceroses and hippopotami. The very large and very small animals, however, are generally left alone, and the greater part of the lion's prey in all habitats is within the 50 to 300 kg weight range. When prey of this size is not readily available, any

animal between 15 and 1,000 kg may be attacked. Those at the lower end of the scale are eaten by individual lions, while the heavier animals are more often killed and eaten by a group. The species of animal, the number and the sex or condition of those that fall prey to the lion vary greatly according to the locality and the season. Schaller (1972b) has made a detailed study in the Serengeti and Manyara National Parks, while Pienaar (1969) has studied the predators of the Kruger National Park and Mitchell *et al.* (1965) those of the Kafue National Park in Zambia. Lions tend to select the more vulnerable individuals of the most available species and while preferences are sometimes apparent when there are numerous prey about, the lion can generally be said to be a catholic and opportunistic feeder.

MANYARA	KRUGER	KAFUE
(Schaller, 1972b)	(Pienaar, 1969)	(Mitchell *et al.*, 1965)
(%)	(%)	(%)
Buffalo 62	Gnu 23	Buffalo 30–35
Zebra 16	Impala 19·7	Hartebeest 16·3
Impala 11	Zebra 15·8	Warthog 9·5
Baboon 6	Kudu 10·9	Zebra 7·3
Gnu 2	Waterbuck 10·5	Gnu 6·1
Others	Others	Others

The figures above record the percentage of animals taken by lions in three African parks. Whilst they reflect to some extent the relative numerical abundance of the prey species they also reflect the availability of the prey, and this is affected by a variety of factors. Where ungulates move over large distances in search of water or grazing, nomadic lions may follow, but the prey available to lions that have established home ranges in such areas may change from month to month. As a result of seasonal changes some prey may become particularly vulnerable to lions: thus giraffes were killed in numbers when they became weakened by a prolonged drought in the Timbavati Reserve (Hirst, 1969). Bushpigs and warthogs were a favourite prey in southern Tanzania while the grass was short, but lions were unable to approach the pigs during the wet season as the long grass hampered a stealthy approach.

Lions are not only opportunistic about living prey but will also scavenge when they can. In the *Acacia* savanna around the National Park Headquarters at Seronera, Schaller (1972b) found that lions kill 88% of their food, while those out on the treeless Serengeti plains scavenge for 53% of their food. The reasons for this are that vultures quickly betray carcasses, sick animals have less chance of recovery on the plains and hunting packs of hyaenas are more numerous. The principle of availability is well illustrated in the Ngorongoro Crater where hyaenas heavily outnumber the lions; here the lions take over a high proportion of hyaena kills and at times rely more on the hyaenas' hunting than on their own. Thus any ready source of food will be exploited by lions and unusual foods may sometimes be important in seeing lions through periods of shortage, and termites, locusts, snakes and

other reptiles, many small mammals, birds and even catfish and groundnuts have been recorded. Small animals become especially important to resident prides in areas where the large ungulates move away for part of the year. They tend to be eaten in great numbers and Schaller showed that Thomson's gazelles were especially vulnerable around Seronera while the large ungulates were absent. These gazelles tended to collect in this area because the edge of the woodland is a sort of ecological weir against the migrating but plain-loving gazelles. In spite of large numbers killed, these gazelles were estimated to account for a mere 2·5% of the total prey biomass eaten by lions in Serengeti. When prey of a more suitable size is available, lions may ignore gazelles and other small prey as they stalk zebras or gnus. Individual lions or prides may prefer a particular prey for a limited period of time; thus numerous zebras and impalas were seen to be ignored by a pride on the Uaso Nyiro in favour of buffaloes. The size of the lion's prey obviously affects the number of animals it is likely to kill in the year. Various estimates have been made and about 30 animals per lion per year seems to be a likely average, with more animals if prey is small and perhaps less if large prey is plentiful and available.

Lions drink daily if the water is there but often go for four or five days without water when it is scarce, but it is also clear that they are able to survive in sub-desert areas where no surface water of any sort is available and Brocklehurst (1931) concluded that the lions living in one arid part of the Sudan must have obtained moisture from the stomachs of their prey. In Kenya, lions have been observed pulling up young *Sanseviera* shoots and chewing the fibres, possibly for moisture, while Livingstone recorded Kalahari lions eating tsama melons, *Citrullus*, for their liquid. Beaton (in Guggisberg, 1961) once watched a mother lioness dip her paw into a narrow rock pool and then let her cubs lick the fur, repeating the movement several times.

Such altruistic behaviour on the part of an adult towards the young is not typical of the lion's behaviour at the kill, nor are co-operative tactics very typical of lion prides hunting, although fanning out and encircling prey are commonly observed behaviour.

The advantages for lions hunting in social groups are most evident when they tackle large prey, and in Serengeti Schaller found that just over half the hunts were conducted by more than one lion. More often than not the single hunter is also watched by other lions. Socialization has led to a crude form of sharing of the hunting spoils and large prey is obviously more easily felled by several lions; there is also the well known sexual specialization of the female as the hunter. Out of over a thousand stalks recorded by Schaller only 3% were made by males.

The killing of an animal is generally preceded by a stalk in which the hunter keeps close to the ground, taking advantage of gullies, grass, bushes and termitaries to approach as near as possible before rushing the prey at close quarters. Animals that are larger than the lion itself are generally unbalanced by the weight of the cat which hooks into the animal's rump with its foreclaws. When a pride is involved the prey's nose or nape may be quickly seized by another lion, but very frequently the hunter itself grabs one or other of these holds as soon as the prey is down. Lions often take the entire muzzle of their prey into their mouth and then suffocate it. This has been noticed to be particularly common when the prey animal is immobilized,

either by another lion or by extreme weakness or sickness. A lioness has even been seen to walk up to a sick gnu and, quietly taking it by the muzzle, suffocate it with hardly a struggle.

Lioness seizing, throwing and strangling a gnu (from photograph)

In addition to actively stalking, lions may ambush approaching prey, a type of behaviour that is most commonly seen at watering places, particularly during the dry season. Meinertzhagen (1957) described a hunt by a pride of two lions, four lionesses and three large cubs in which both techniques were used. Originally bunched together, the males, cubs and two females separated from the two other lionesses and started a wide detour to approach a herd of 15 zebra about 500 yards away:

> "the two lionesses left behind separated and took up crouching positions some 100 yards apart, both intently watching the zebra. Meanwhile the main body of lions had reached a position where the zebra should have got their wind. Suddenly up went the zebras' heads in alarm and they stampeded down wind, while the lions with cubs lay flat with only their heads erect. The herd of zebra passed between the two lionesses but only some 20 yards from one of them. As the herd of zebra got more or less level with the lionesses they suddenly stopped and looked back. At that moment, the nearest lioness launched her attack at full gallop and sprang at her victim, it was all over in a moment."

The implication that the lions were aware of the direction of the wind in this and in other descriptions of lion hunting have not been borne out by Schaller's carefully quantified observations. Lions are primarily visual hunters and they ignore the direction of the wind, and in spite of being three times more successful when stalking gazelles upwind, they do not seem to learn from their failures. Long detours are not uncommon even in stalks by

individual lions. They will often try to cut prey off by running ahead of it, thus anticipating its line of flight and they are also quick to take advantage of the consequences of other pride members hunting behaviour; this can be illustrated by an incident where a large herd of Thomson's gazelles were seen coming down to drink below a strolling lioness:

> "She appeared to take no notice of the herd until the gazelles were between her and the reed covered swamp. The lioness then rushed forward into the herd with a terrific speed, scattering the panic stricken Tommy in all directions. At least 20 of these little animals were chased into the reeds where they could only move in short leaps covering very little ground. As soon as this happened other lions and lionesses and half grown cubs poked their heads up and at once ran over to the trapped gazelles. Eight Tommy were killed in less than a minute." (Cullen, 1969)

Apart from the tendency for individuals or groups to fall out and thus encircle prey there is no concrete evidence of truly coöperative hunting behaviour.

Although a lion may achieve the speed of 45—60 km per hour in a rush, it has no stamina and will quickly give up a chase, panting heavily after a few hundred metres. As a measure Schaller has pointed out that the heart of an adult male lion is only 0·46% of its body weight (a female's 0·57%), whereas the hyaena, which can sustain long chases, has a heart nearly 10% of its total weight.

Lions prefer to hunt in the evenings about dusk or at dawn and Schaller also noted a major hunting peak between 2 and 4 a.m. Although the moon has little or no influence on their activity, their hunting is markedly more successful during moonlight betraying the importance of sight in hunting. They are however able to scent-trail other lions and probably use this method of hunting more during the rains, when long grass obscures their vision (and that of the observer). Sound must also play an important role during the rains and on dark nights.

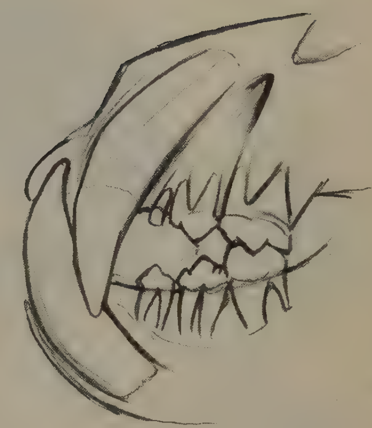
Occasionally lions kill more prey than they can eat, particularly when they get into a stock-yard or cattle *boma* or in other situations where the prey animals present easy targets. Lions at Ishasha killed numerous topi one dark and stormy night without eating from any of them (Allibhai, personal communication). A lioness in Tanzania was seen to kill four gazelles within an hour and, having eaten one, dragged the other three under a tree, where she sat guarding them. Lions often have to guard their prey from a variety of competitors, hyaenas, jackals, vultures and storks, but very occasionally lions attempt to cache carcasses in the branches of trees, which suggests relic behaviour similar to that found in the leopard. Another interesting report from Tanzania (T.G.R., 1938) concerned two lions that had dug a hole in which one buried portions of an eland while the second guarded other remains from the vultures. Burying or the scraping of earth and debris over the remains of a kill is found in many felids, but in lions it is commonest when they abandon a carcass after eating their fill. The viscera or stomach contents are occasionally buried before the carcass itself is eaten. Such behaviours might represent non-functional vestiges from an original pattern in which kills were cached and revisited, as in the leopard, or, as Schaller suggests, pawing may function as a visual-olfactory marking of the kill site. Lions seldom revisit kills after leaving them, although a pride may spend several days in the immediate vicinity of a large kill.

In Ngorongoro, 25 adult lions fed on an eland and ate it up completely in a few hours but then lay around for four days hardly moving and others have been seen to spend even longer periods without showing any interest in feeding. In the same locality two eland bulls were killed together and fed a pride of 30 lions. (On this occasion, a lioness was seen to swipe a vulture and while holding it down between her paws was pecked in the face, after which she released it, apparently unharmed.)

The largest prey are not infrequently tackled by the males and Cowie (1961) described two male lions attacking a tame subadult rhino that lived near one of the Tsavo lodges where an apparently amicable indifference existed between the rhino and the resident pride. One night the warden was alerted by the rhino's squeals and found it on its side with one lion fastened to its

cheek and another across its ribs biting the neck. Using his car to frighten off the lions, the warden allowed the rhino to regain its feet only to see it pulled down again by a single lion that reared up and grabbed it across the back, a feat of strength that was achieved without apparent effort. Adult hippopotami are likewise thrown down onto their backs and killed by bites in the throat or chest. Crocodiles, which used to be a common prey of lions on the Rufigi River were killed at the throat but were generally only eaten from at the base of the tail. Giraffes, even adult bulls, have been seen to be killed by two or more lions, and a lioness was once found crushed beneath a dead bull giraffe. Stories that giraffes are ambushed from trees are unsubstantiated, but a male lion has been seen to leap down out of a tree in which it was resting on to a lone buffalo calf. Guggisberg described how a 400 lb heifer can be carried over a high fence by the lion vaulting over, holding to the cow's neck, and having swung its own back-end over, dragging the cow after it. Lone buffalo bulls are not infrequently killed by lion prides and sometimes surprisingly little resistance is put up (see Vol. IIIC). Lions have been photographed feeding on a carcass with other buffaloes watching unconcernedly from a few metres away. On numerous other occasions, particularly when the victim bellows in distress, other buffaloes have charged lions without hesitation. Where only one buffalo is involved there may be mock charges,

but groups are often sufficiently determined to force lions to flight or up trees.



Occasionally less formidable prey manage to intimidate or throw off attacks by lions. A herd of oryx has been observed to terminate a lioness's stalk by facing her, and grazing gnus have been seen to turn on a stalking lioness and pursue her in a tight bunch all lashing their tails and shaking their heads. Predatory behaviour may be entirely subverted in an artificial situation and Guggisberg recounts the experience of a film crew who surrounded an enclosure with cameras to film a lion making its kill; after first introducing the lion a gnu was released. The lion jumped up and ran round and round closely followed by the gnu and nothing would induce the lion to kill it. Even in the wild solitary gnus have occasionally been seen (and photographed) turning upon their attacker; the outcome varies, the gnu may be killed or sometimes the lion gives up or flees.

Where warthogs are common the lions regularly dig them out of their holes, although it is not unknown for the pigs' tusks to cause damage or death. In Uganda, three cubs were killed in 1959 by a pig they had tackled and three years before an adult male lion was found dead of a heart wound beside a badly mauled warthog.

After killing its prey, the lion will sometimes lick the fur of the animal meanwhile purring loudly, then the skin and fascia are sliced with the sharp scissor-cut of the carnassials and joints are torn apart by the canines and chewed. Relatively small pieces of meat are pulled off by the incisors and swallowed and bones are often rasped clean by the coarse sand-paper action of the tongue. The amount of meat eaten at a sitting varies widely, but Schaller estimated an average of 16 kg. One male was estimated to have eaten 33 kg in one night.

Cubs begin to make playful stalks from the age of about one month and they can sometimes be seen creeping up to or chasing birds or mice while the adults sleep. A large part of the cubs' play seems to consist of such hunting behaviour, although the object of a stalk or chase is often another cub or some object like a feather or a piece of wood. Swatting or pawing of another cub's rump is also common and this may turn into a wrestling match such as is usual with all young cats. Lionesses often play with their cubs and will participate in the cubs' chases as either the chaser or the chased. After watching cubs playing with a tortoise, I thought that the natural movements of the unfortunate reptile must be custom-built to provoke the young cats' predatory behaviour. Leonine fascination with chelonians seems to extend into adulthood too; I once picked up a nearly intact turtle shell in a river-side thicket and was surprised to find it still hot and with traces of unclotted blood on its neatly scooped out and clean interior. Until I had joined my companion across the river bed I failed to notice an adult lion watching me from the thicket as I carried off the shell. As a sable cow had been killed by lions in the immediate vicinity only two nights before, he was probably well fed.

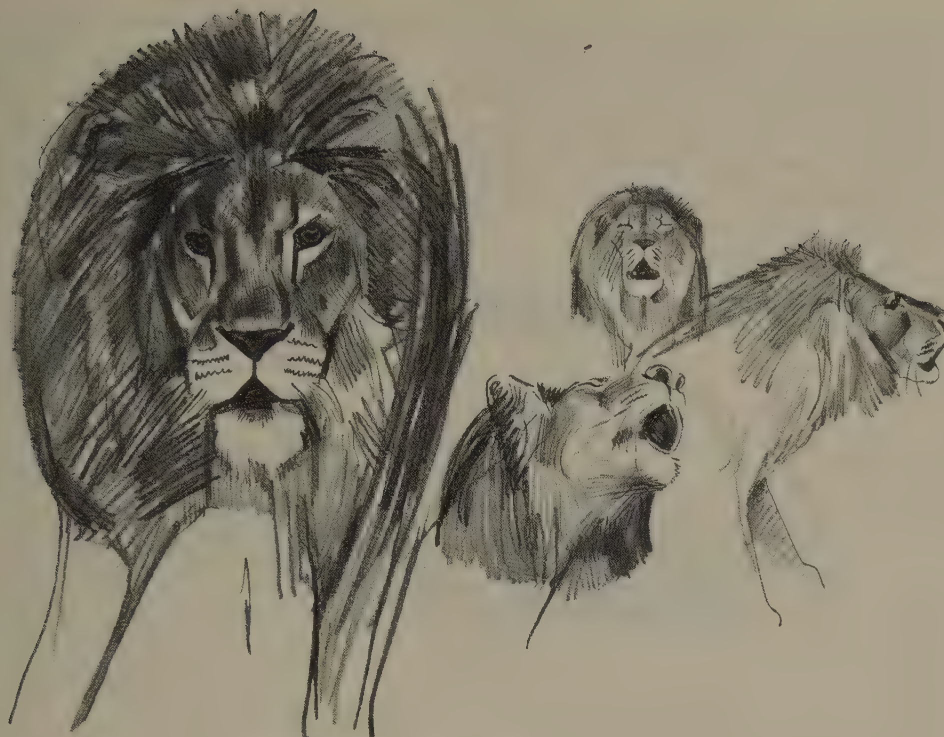
Lionesses and cubs frequently toy with wounded animals and when the cubs are allowed to participate this is often mistakenly interpreted as a lesson in hunting. Such behaviour is generally a sign that the lions are well fed and secure. Animals that could be killed for food are sometimes released or allowed to escape. For instance, a lioness was observed lying up in a

patch of grass with her cubs whence she successfully stalked a waterbuck and a warthog in succession; in each case she merely bounded up to the animal without killing it (Guggisberg, 1961). Like domestic cats, lions will capture and paw their victims; or, after toying for some time with a gnu calf, a jackal or some such animal that has come within reach, will eventually permit it to run off. Tail tips are a favourite play object for cubs and they will pat and chase the gently twitching tail of an adult for long periods.

Human beings probably see the lion's relatively patternless face as more expressive than that of, say, a leopard. Facial movements and their communicative functions are very similar in all felids (p. 406) but small changes in the lion's eyes, lips and ears are emphasized dramatically by the subtle tonal emphasis of these features.

The eyes of lions were particularly carefully rendered in Assyrian and Ancient Egyptian sculpture, and onlookers in zoos are often impressed or betray disquiet under the stare of a lion, a feeling that is shared even more intensely by those who have encountered lions at close quarters on foot; the initiation of young hunters in parts of Africa used to depend upon the young man facing the lion's awesome look (Frobenius, 1954).

Expressions function at close range and are obviously more important in a social than a solitary species. Licking and head-rubbing, which are also seen in other cats, are especially noticeable in lions. The head and neck are the main target for social rubbing, which seems to serve an appeasing function.



Both sexes of lion roar and it would be difficult to imagine a more impressive form of self-advertisement. Some of the functions of roaring suggested by Schaller are the delineation of pride areas, the means of contact and relocation and a device for social bonding. Roaring consists of eight or nine reverberating roars, which can be heard up to eight km away on a still night, followed by a declining series of grunts, averaging about fifteen, but which can occasionally number fifty or more. Two or more lions may synchronize their roaring and they frequently elicit answers from other lions. Schaller described a dying lion grunting in response to distant roars, even though he was too weak to raise his head. Contact between the lions of a pride is sometimes made by means of a soft muffled roar, uttered with the head lowered instead of raised. Miaowing is often a distress call and in adults it signifies mildly defensive threats or frustration. Males miaow while copulating and a variety of other calls have been described; "puffing" as a greeting is commonly used by females towards a male, while "humming" and "purring" are expressions of contentment. As with most carnivores, growling is a warning signal and a startled lion lets out a very characteristic "woof". Joy Adamson, in a uniquely intimate relationship with her tame lioness, was able to note that the animal's paws became damp when she was nervous. The same lioness was also noticed to defaecate several metres away from the game path that she habitually used. Lion dung seldom lies about for long as it is eaten by hyaenas, jackals and vultures or is buried by dung beetles. This female

showed no interest in the dung of other carnivores but was fond of rubbing herself in rhino and elephant droppings.

In hot weather, lions prefer to lie under shade or on wet sand and moist soil if it is available. Butler (in Pease, 1914) saw a lion on two successive evenings coming to a pool in a river bed, where, after drinking, it scraped up a heap of wet sand on which it reclined its chin.

Captive lions have lived for nearly thirty years, but the average life of zoo lions is about thirteen years, an age at which wild lions could be expected to have already declined. Further study of ageing in wild lions may bring greater precision to our understanding of pride dynamics. Before Schaller's study on the Serengeti lions, the understanding of the social structure in lions was confused and, although the "pride" has been retained to describe the lion's basic social unit, Schaller has been at pains to define his terms.

Lions have sufficiently plastic social systems to adopt a wandering or a settled existence in response to the exigencies of their environment. Schaller reserves the term "pride" for a group of resident lions living in a definite "pride area". By contrast there are nomadic lions that wander over a much more extensive region, these animals are best designated by the term "nomad group" and their movements define a range rather than a pride area. Prides contain three to forty lions (with an average of fifteen on the Serengeti) but for a lot of the time a pride may be fragmented into subgroups. The number of lions in these tend to be correlated with the size of the dominant prey available at the time, the smaller and more diffuse the prey the smaller the groups of lions.

One of the most important findings to emerge from Schaller's study is that the lionesses and their female offspring provide the continuum for a pride and that male attendants and siblings should be regarded as a distinct and more transitory part of a pride's structure. The females in a pride are all directly related and associations between mothers that whelp together and cubs that grew up together are close and durable, which suggests that the social system has developed around the mother—young and sibling to siblings links. The mature males in a pride mostly join it as fully adult nomads but generally do so after expelling older resident lions that are in decline.

The earliest associations are amongst cubs that belong to the same litter

or age-group; when the male cubs reach the age of two-and-a-half to three-and-a-half years they usually become peripheral and then leave the pride to become nomadic, a condition that probably lasts for many years, particularly if an individual lion remains solitary. When long-established male regimes are displaced, this is generally enforced by two or more lions that have already formed a companionship (possibly as sibling cubs), indicating that there are advantages in close associations for both sexes. Companionship between animals of the same sex are closer than those formed between males and females within a pride and companions commonly gang up against any strange animal of the same sex coming into the pride area. The hostility of pride lionesses is towards strangers of their own sex and males likewise chase off foreign males, which serves to maintain the pride's integrity. Recruitment within the pride differs along sexual lines because the main source of female replacements is the offspring of the pride itself. Males, on the other hand, as they age and decline, tend to be replaced by outsiders. During the seventeen years that Guggisberg followed the fortunes of a pride in the Nairobi National Park, he watched four successive sets of males: some were pairs, some single. Following up Schaller's study of two Seronera prides Bertram (1975) estimated that males live half as long as females and he recorded seven changes in male regimes in as many years, the longest tenure being three years by six lions, the shortest being a matter of a few months by single lions. Describing the differentiation of sexual roles Bertram noted that it is the males that are primarily responsible for maintaining a pride territory by urine marking, patrolling and above all by roaring.

Lions in national parks are often in an ideal habitat with reasonably stable conditions and assured year-round sources of food. Outside the parks there tend to be seasonal fluctuations in the lions' food supply and considerable human disturbances. Under such conditions the formation of stable prides is likely to be frustrated by the lions' need to follow prey and to travel over an extensive and little known range. Scattered prey animals encourage the fragmentation of lion groups into singles, twos and threes. In contrast to the territorial intolerance of prides, lions living in this way will readily associate with other lions if they find themselves concentrated in a locality because of a temporary abundance of prey, but will also disperse equally easily. After

long-term fluctuations in ungulate populations, the lions' extensive wanderings soon reveal where herds have recovered, after which the lions may come to associate on the more permanent and exclusive basis of a pride.

After the formation of the Nairobi National Park, lions were at first observed to be relatively tolerant, but with the passage of time it was noticed that they became much more territorial (Cowie, 1961). This was probably a case of nomadic lions settling down into prides as the direct result of their newly found security. Most nomadic groups are made up of pre- or post-mature males and are sometimes called bachelor prides. Solitary nomads are more often than not subadult. Less than half of the nomadic groups studied by Schaller contained females and he also demonstrated that nomadic lionesses had fewer offspring than their resident counterparts living in stable prides.

Established prides generally contain several adult lionesses together with their subadult or juvenile young and one to four attendant adult males and Bertram estimated that the average pride contains 60% cubs. Schaller lists 37 as the largest number of lions in a single pride but a group of 75 lions is on record. However, without background knowledge it is not possible to guess at the status of such an exceptional aggregation.

The density of lions in a particular area will depend very largely on the year-round availability of prey and, in settled areas, on the attitude of the people. In the Manyara National Park the prey biomass reaches up to 7,200 kg per sq km and the record of one lion per 2·6 sq km must be near the optimum (Makacha and Schaller, 1969). In the Serengeti there is a density gradient of one lion per 6·3 sq km in the open woodlands, one per 8·3 sq km in the heavily poached "corridor" and an overall density of one per 12 sq km, including the extensive plains which are seasonally devoid of prey and therefore also of lions. Pride territories in Serengeti range between 20—100 sq km (Bertram, 1975).

In many settled areas of East Africa lions are occasional visitors. There is often a seasonal pattern to this, as on the Iringa Plateau, where every year a few cattle are killed between August and November, after which the lions are not seen again until the following year. Such wanderers are nomadic lions and it is possible that their overall range during one year might cover 5,000 sq km. In such cases the size of the range may reflect scarcity of prey or perhaps harassment from humans. On the other hand, the closed social system of the pride only develops in undisturbed areas where there already is adequate food and water throughout the year.

Groups of lions have been watched interacting with other groups for many years and there have been various interpretations of their behaviour. However, without knowing the individuals in a group or their social status or range, the meaning of such observations must remain obscure. In his pioneer study Schaller used new darting techniques and has revealed social structure in a way that was formerly impossible. Schaller has defined a pride area as being a territory, in the sense that other lions tend to avoid it or are driven from it by its owners. The males generally assume a dominant role in the area that is used by the lionesses, although some range more widely and a few associate with more than one pride. Overlaps may be so extensive that no portion of a pride area is reserved for the exclusive use of one pride alone.

The advertising function for the roar in territorial behaviour and the lion's readiness to retreat outside its own area are well demonstrated in Schaller's observation of marked individuals in his study area. Two males from a neighbouring pride were seen eating a zebra with a female which was in her own home area. When two other male lions approached the first pair fled, roaring as they went. The new arrivals were known to belong to a still more distant pride and their reaction to the roars was also to flee, leaving the resident lioness in sole possession of the kill. On another occasion seven lionesses of the same pride roared as they passed across country that was usually occupied by a neighbouring pride; several lionesses answered immediately from a rocky hill nearby and the intruders abruptly returned towards their own area. In the same locality an old pride lion was seen to chase a lioness away, after which all the members of the pride roared and, on another occasion, two males in pursuit of a trespassing male stopped every so often to roar. Guggisberg saw three Rutshuru lions put to flight at the sound of another lion's roars.

While the pride lion's confidence may be bolstered or sapped according to how near or how far it is from its own home area, this seems not to be the only determinant for its behaviour. That greater numbers may win in spite of trespass is illustrated by Schaller's observation of a lioness finding and eating from a dead zebra in another pride's area. When she left (as it turned out to fetch her cubs), vultures betrayed the carcass to three of the lionesses and their cubs that lived in the area. Returning nearly two hours later with her cubs the intruder roared softly several times without receiving any answer. Instead two lionesses of the resident pride approached her silently. She retreated and went to her own pride where, somehow, she induced six lionesses to follow her, whereupon they all trotted towards the carcass and, chasing off the residents, ate the remaining meat. Such an incident could well have culminated in a fight and there are in the records of the East African Game Departments and National Parks very numerous references to fatal combats, many of which appear to be territorial in origin; as, for example, the following report.

> "Two lionesses from the Athi basin area of the Nairobi National Park came up as far as Eland Hollow and made a kill but were then found by the lionesses who live in that area. A roaring match started, but the interloping lionesses stuck to their kill. Two male lions heard the uproar and galloped across from about two miles away. One immediately attacked an offending lioness and killed her, the fatal bite being in the neck. The remaining strange lioness retired back to their own area." (KNPR, 1965)

On another occasion in the same park, two male lions were seen to corner a young lioness, which was eventually caught and killed after making frantic efforts to escape. The carcass of this lioness was later seen being eaten by another young lion and lioness which had been her companions.

Defence of territory is by no means the only reason for fighting and it is probably true to say that every meal represents a potential upset for the fragile social structure of these powerful cats. At the kill it is every lion for itself and the dangers are particularly great if the prey is small. As early as 1856 Anderson reported a lioness killed and eaten by a lion immediately after the

two animals had killed a young springbok. The same author reported lions killing a wounded companion and there is a more recent account of a lion eating its shot companion. Stevenson-Hamilton (1954b) found four cases of cannibalism in one locality in the course of three months; in three cases males ate their male companion and in the other two lionesses ate a male.

Cowie (1961) described a fight between two lions that went on for ten hours in front of a lioness and ended in the death of both participants. It may be tempting to see such a fight as contest for the female, however, it is not possible to interpret such observations without background knowledge of the individuals. That her presence may have been incidental to the fight is suggested by the many years of observation by Schaller and Bertram. They did not see males compete for a female and Bertram has stressed that pride stability depends on this.

A female in oestrus may actively solicit a male and both males and females sometimes exhibit a definite preference for an individual while courting. Nonetheless, an oestrous female will mate with several males if she is not closely followed by a particular consort, she is also more likely to tolerate strange males while in oestrus. Oestrus lasts anything between one day and three weeks and recurs at intervals of two weeks to sixteen months, but about one in five oestrus periods result in offspring (Bertram, 1975). The female

betrays her condition by scent and by a general restlessness, an erect swishing tail, by cheek rubbing and presenting herself in a crouched position in front of the male. Males sniff at the female's genitalia, lick her rump or the nape of the neck, after mounting they may grimace with drawn-back lips or make yowling noises; however, they may also be silent over much of the procedure. Aggressive or defensive threatening by the female punctuates most matings and she may frequently break away or attack the male. Notwithstanding this, males are often very persistent—in the Dresden Zoo two lions mated 360 times in eight days and Bertram estimated that a wild lioness mates about four times an hour while in oestrus. Cooper (1942) recorded that for every successful pregnancy in captives there had been 1,500 copulations, so that the reproductive efficiency of lionesses can be seen to be very low. Because mating is promiscuous it does not create male—female bonds and the extraordinary frequency of mating presumably serves to reduce the possibility of competition between males.

Gestation lasts 100 to 119 days and one to nine young may be born, although the average number is two to four; very balanced sex ratios have been recorded.

Although there is no overall breeding season, it is not uncommon for two or more lionesses within a pride to have their cubs at the same time. As females within a pride will suckle one anothers' young, there are clearly advantages for the young being born at the same time, and Cowie (1961) described how four young cubs survived their mother's death (from an abdominal puncture inflicted by a gnu) by suckling from another female that was lactating at the same time.

While sibling lionesses are quite likely to come into oestrus together, it is also possible that females might be synchronized by vicissitudes common to the whole pride, such as the death of all the cubs. There is, however, considerable leeway as a lioness gives milk for five to eight months and the young feed exclusively on milk for only about two months.

Bertram found that there was a dramatic drop in both the birth and the survival rate of cubs during the six months following the installation of a new male regime, which he suggested was due to abortion and direct killing of the cubs by the new lions. Bertram regards this destruction of the former regime's offspring as a form of indirect competition between males which favours the offspring of the infanticidal lions and hence might serve to fix this peculiar specific trait.

The young are generally born in a secluded spot among rocks or in some complex of thick vegetation such as a thicketed termitary or a reedbed. At birth cubs weigh between one and two kilogrammes and are blind for anything between one day and a fortnight. Their eyes are grey at first, turning yellow at about three months. Their milk incisors appear at about three weeks and they have lost their milk teeth at about the age of one year.

The cubs remain hidden for six to eight weeks, by which time they are strong enough on their legs to follow the mother and the rest of the pride. The cubs follow the mother when she grunts and moves slowly, but they tend to stay put when she moves rapidly and silently.

The first three months of life are hazardous for the cubs and they may be killed by various predators; hyaenas, leopards, martial eagles have all been

recorded. In the cases in which adults kill cubs, strangers to the pride or recently assimilated males are likely to be responsible.

The mother's behaviour also presents problems and Schaller has remarked that the response of a lioness to her cubs is so finely balanced between care and neglect that their survival is threatened whenever conditions deteriorate. He provides an apt illustration of a lioness catching a gazelle and fetching her cubs to the site. The cubs failed to follow her down an embankment, but after waiting ten minutes they apparently heard her eating and ran up, upon which she grabbed the carcass and fled. It was only after a considerable amount of mutual aggression that they were permitted to eat.

Some lionesses are known to be unsuccessful mothers. Guggisberg singled out a well known Nairobi Park lioness, "Blondie", in this respect and Schaller witnessed a Serengeti lioness leaving one of her three cubs behind in a ravine and never returning for it. She subsequently also lost the others.

Adult lions will often drive other members of the pride off a kill, including young cubs and when the prey animals consistently fail to provide a surplus of meat the cubs may not get a share, with the result that they starve. On the other hand, in matters unconnected with food, mothers occasionally display a well-developed protective concern for their cubs. An example of this is illustrated by a lioness and her cubs joining other members of the pride across a river in which there was a strong current; the lioness dipped in a paw and then

> "calling her cubs to her side, the lioness gathered them so that they pressed close to her body. The family entered the water cautiously. The current pushed the paddling cubs up against their mother's side and shoulder, ribs and flanks. As the lioness reached the near bank the third cub slipped back and in a second was being washed downstream. The mother pushed the first two cubs on to the bank, then turned down and plunged into the water. She reached the third cub in a couple of splashing leaps and her jaws closed gently round it." (KNPR, 1966)

The cubs' growth rate tends to vary as starvation or food shortages have a stunting effect on growth, but an average weight at the age of 15—17 months is about 50 kg and goes up to 100 kg by the time the males are two years old. Sexual differences are already clear by this time, not only in larger size but also in broader heads and in the ruff, which may start as early as six months. Up to the age of about four years, when they are mature, subadults are distinguishable by snubby, less angular muzzles and a generally slighter body build.

On the basis of these distinct field characteristics, Schaller kept records of male—female and adult—subadult ratios in the Serengeti. He found highly significant differences between the woodland lions (predominantly organized in prides) and the open plains lions (mostly nomadic). Half or fewer of the former were adults and there were two lionesses to every lion. The subadults, on the other hand, had an equal sex ratio and made up a quarter of the population. A higher ratio of fully adult animals (57%) and an equal sex ratio betrayed that the plains lions were less successful breeders.

An emigration of subadult males from prides in the woodlands is implied by the presence of two subadult males for every female subadult in the plains.

Crandall (1964) described the development of a homosexual relationship within a group of five captive males that were confined together in an American zoo. This group started to quarrel as they became mature and one dominant male segregated a smaller pale animal, not allowing the other three to approach it, a situation which finally became accepted routine with minimal disturbance. On the death of the dominant male, the pale male was accepted into the remaining trio without any sign of further exclusive attachments. This illustrates the persistence, even in the restricted conditions of captivity, of the lion's tendency to form bonds with individuals of its own sex.

On Serengeti, Schaller estimated that 67% of the cubs died each year mostly through abandonment, although starvation, predation and adult violence all account for numerous deaths. By contrast, he computed an annual adult death rate of 5·5% through aggressive interactions with other lions, through old age and disease. Births gave an 11% annual increment. Apart from the amount of food available to the lions in any particular area or season, man is today the principal controlling factor outside the National Parks.

Among the mishaps that can befall lions are grass fires, floods, and wounds from resisting prey. Cowie (1966) reports cubs killed and partly eaten by soldier ants and Heye (1927) shot a lioness that leapt into a lake in front of him. He found her entirely covered in soldier ants with thousands in her nose, throat, eyes and ears. A lioness with cubs was seen baiting an Egyptian cobra and Downey reports a large python killed by lions after it had attacked one.

Porcupines represent another hazard for lions, the quills sometimes working into some vital organ or very often disabling the lion for hunting. Fatalities inflicted by resisting prey are generally from the more heavily horned species, buffalo, roan, sable, kudu and even warthog. Elephant have also been seen to kill lions and Guggisberg records that the remains of a lion were recovered from a crocodile's stomach.

Lions are often heavily parasitized (see table below). The much publicized lioness Elsa died of Babesia tick fever, carried by the ticks, *Haemaphysalis leachii* and *Rhipicephalus sanguineus.* Trypanosomes have been found in their blood. Fosbrooke (1963) described an exceptional plague of *Stomoxys*, blood sucking flies that bred in mud of the Ngorongoro Crater lakes. These flies were so numerous in 1960 that they caused the emigration or death of 55 of the 70 lions living in the crater. In South Africa, lions have died of anthrax (Pienaar, 1961).

LION PARASITES	
Ticks	*Rhipicephalus carnivoralis* *Rhipicephalus sanguineus* *Rhipicephalus simus* *Haemaphysalis leachii*
Flies	*Hippobosca* spp. *Stomoxys calcitrans* *Glossina* spp.
Worms	*Taenia gonyamai, Taenia bubesi* *Neolinguatula nuttali*
Blood parasites	*Trypanosoma congolense* *Trypanosoma brucei* *Hepatozoon canis* (protozoan) *Brucella abortus* (bacterium)

Lions compete with other predators for the available prey, but the more numerous these are the more likely are the lions to appropriate their kills. At times cheetah lose a high proportion of their prey to lions and where hyaenas are numerous and kill their own prey they often lose it to lions. One subadult Serengeti lion was seen to appropriate a carcass from 17 hyaenas, and two lionesses took one from 31 hyaenas.

The nocturnal hyaenas may be less confident during daylight and, as most lion—hyaena interactions have been observed by day, it is possible that hyaenas may gain the upper hand more frequently at night. Hyaenas attempting to drive lions away concert their movements with harsh growling noises and massed rushes, their hair erect and their tails held perpendicular. Stephenson (1966) described eleven lions in the Mikumi area which were driven from their kill by a pack of eleven hyaenas. The hyaenas were in tall grass surrounding the kill and made noisy concerted rushes within a few yards of the lions. Eventually four young lions moved off, followed by baiting hyaenas, the remaining young lions and lionesses were not long in leaving the male, which appeared quite indifferent for a time. The hyaenas resumed their rushing and after four or five such demonstrations the lion moved off followed by the pack, but the lion turned on to his assailants in the long grass to the accompaniment of tremendous noises. A few minutes later all the hyaenas were gathered around the kill. Very occasionally a pack of hyaenas will actually kill a lion. Lions have been photographed killing and even eating hyaenas and they have also been seen to kill cheetahs and leopards.

Oddly enough, vultures can be of some significance as competitors. One pride of lions was seen being kept off their kill by an angry buffalo, while the vultures in the meantime dismantled the buffalo's dead companion in a surprisingly short space of time; vultures and jackals coming too close to a feeding lion are sometimes attacked and killed.

In addition to appropriating kills made by cheetahs and hyaenas, it is not unknown for them to take over game captured or killed by humans and in prehistoric times lions might well have been a nuisance to those hunters unable or unwilling to keep them off. On the other hand, the early hunters must also have learned to intimidate lions and so acquire a source of free meat. In the Kalahari the Bushmen used to do this and Smith (in Kirby, 1940) found that one tribe actually protected the lions because of the quantities of fresh meat they provided.

As recently as 1928 local people in Bugerere, Uganda, got to know the habits of a resident lion and systematically helped themselves to part of its kills, apparently with impunity. This state of affairs continued until some photographers seeking close-quarter portraits shot and disabled this very accommodating lion.

Lions have been reared or habituated by man since the very earliest times and in Ancient Egypt the town of Leontopolis took its name from the lion

cult that flourished there. The most important event in the Egyptian calendar was the Nile flooding, represented by the hieroglyph of a lion's head. This probably had astrological connotations but animal cults had reached such a point in pre-Christian Egypt that elaborate ceremonial funerals were held for dead lions. Ramses II, like the royalty of many nations, kept lions as an attribute of power but he also had one named Auto-m-nekht which was said to have been trained to run beside his chariot horses and knock down anyone approaching the royal conveyance. Ultimately, the great menageries that had been built up by the Ptolemies in Alexandria were destroyed by the Christian emperor Theodosius who banned all animal cults in A.D. 384.

In classical Greece a Phrygian goddess, Cybele, became the object of a widespread cult. This Asiatic goddess personified the earth in its primitive and savage state and she it was who had dominion over the wild beasts, so she was symbolically represented as being drawn in a chariot pulled by two lions. The followers of Cybele were known as Corybantes and they were given to self-flagellation while dancing to drums, cymbals and the clashing of swords and shields. Some of the priests of this cult, the Galli, travelled far and wide, accompanied by a tame beast, often a bear or a lion, which was used in the exorcism of evil spirits. Variations of this shamanistic cult are ancient and have been very widespread. At about the turn of this century, Pease (1914) encountered a travelling exorcist in Algeria; this man was carrying a great, blind lion about on the back of a donkey. The beast was claimed to be an effective cure for hysteria when introduced into the patient's room!

The Romans used lions as sacrificial beasts, Julius Caesar had 400 ceremonially killed to consecrate his forum and on the nomination of Germanicus as consul 200 lions were killed. Their use as executioners is best known in the story of Daniel, but even in Mediaeval Europe the practice was not unknown; Ludwig IV of Bavaria was supposed to have fed a monk to the lions in his menagerie.

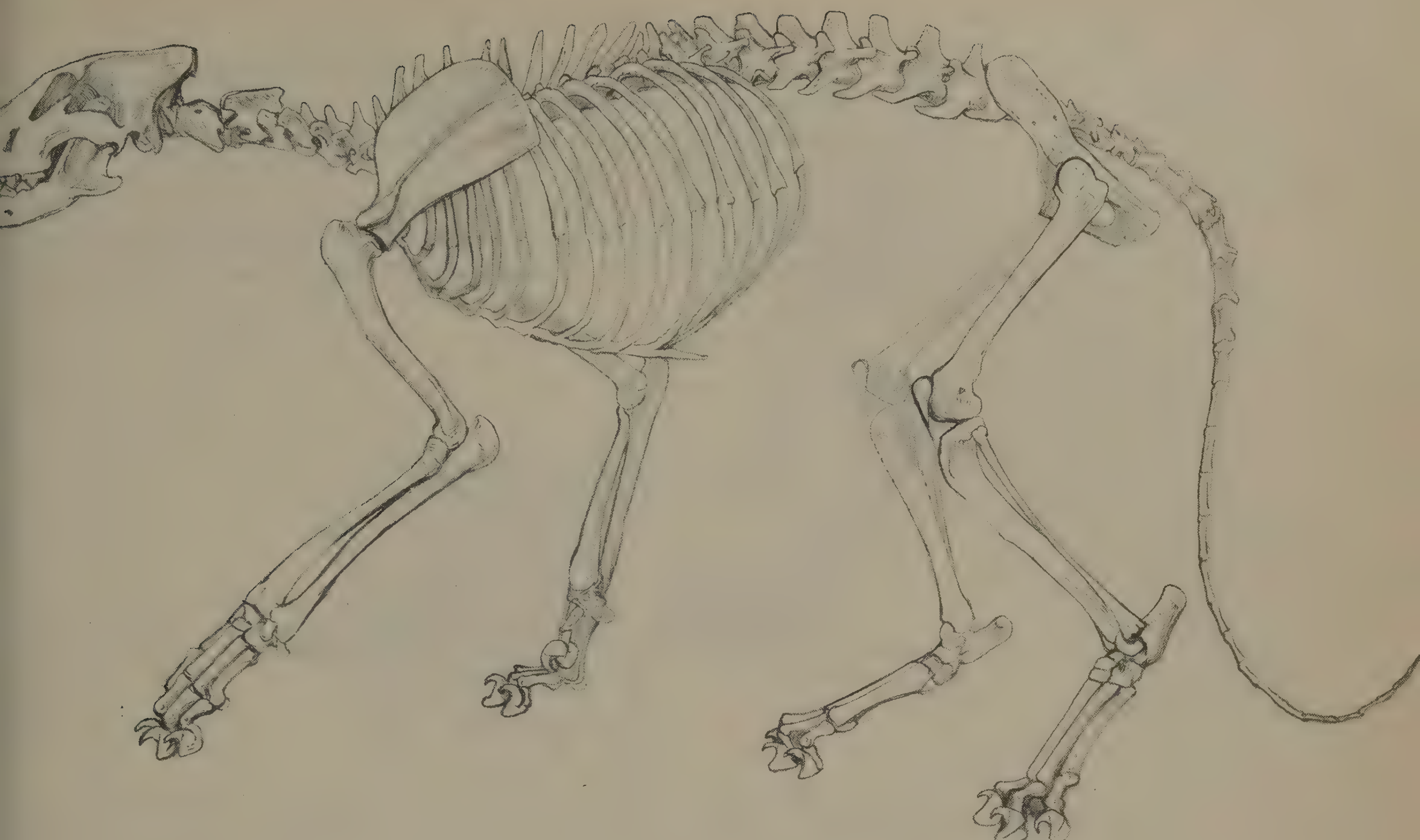
Not only kings have used lions for social and psychological effect and lion-taming acts in circuses still draw crowds. Circus lion-tamers exploit the lion's natural respect for gestures of dominance, while the success of more domestic lion-rearers is probably influenced by the close ties formed between a cub and its mother or foster mother and between siblings. Over the years a number of game wardens and other local residents have habituated lions by feeding them or have reared lost cubs. In 1932, a professional hunter, Alan Tarlton, tamed a wild pride of twelve lions for the benefit of a film company. Through regular feeding from a truck the lions became so used to Tarlton that he could walk amongst them while they fed. Because he believed the human voice had a soothing effect he always talked to them. The greatly publicized activities of more recent generations of lion rearers, rescuers and tamers suggest that the cult of Cybele is far from dead in the West today.

There are numerous stories in East Africa of witches or wizards associating with lions and it is possible that people living in areas where lions were numerous sometimes acquired some control over them. Such individuals would have earned thereby a reputation for magical powers and, in those societies that were governed by fear of the supernatural, anyone associating

with a wild lion could clearly wield power. Even more powerful were witches or secret societies that killed people at night in the guise of spirit lions or lion-men. In the central region of Tanganyika such lion-men had an established reputation. In 1920, a youth was caught with artificial lion paws and dressed in lion skin. He and his employers were convicted for murder after a total of some 200 faked lion killings had taken place in the Usure area.

For over ten years parts of the Singida district were subject to an organized *mafia* of lion-men or *Mbojo* which, like most terrorist movements, escalated as revenge bred revenge. By 1947 one hundred and three deaths had been reported and the government mounted a concerted effort to catch those responsible. Wyatt (1950) gave an account, based on official sources, of the ensuing trials which were a *cause celèbre* at the time. It transpired that children had been kidnapped, mentally degraded with the aid of hashish and trained over a period of years to kill with knives and claws. Dressed in lion or baboon skins, these *Mbojo* were hired out for punishment or revenge.

The terror inspired by supernatural lions has its origins in the dangers people often face from real lions in areas where they are common. The odd human casualty still occurs but it is not long ago that lions in some localities regularly fed on people. In some areas modifications to the architecture of huts were said to have taken place in order to deter lions from breaking in,



which is itself some indication of the past prevalence of attacks. In the Lindi district, 140 people were eaten in the course of a few months and 20 people taken in 1935 were the victims of a pride of five subadult lions all in good condition. In Ankole, two lions were held accountable for 124 human lives in 1925. During the second world war a total of 153 people were eaten in the sub-chiefdom of Wangingombe alone, the lions travelling in two prides, one of five the other of eight lions and there are other numerous instances of man-eating in the annual reports of East African game departments. Bourlière (1955) noted that the eating of people by Rutshuru lions in 1904 and 1905 coincided with a big reduction in the herds of topi and kob.

As I remarked in an earlier volume (Vol. I, p. 20) the eating of people is sometimes correlated with the rains. Other foods are scarce, scattered or very difficult to approach because of the long grass. Flooding may put lions into close contact with villages on islands of higher ground, while human "drinking seasons" may render already easy prey even more vulnerable. If man-eating lions are not shot at once, the general principle of availability operates for humans no less than for any other prey. Yet man-eating still tends to be regarded as unnatural. It has evoked extraordinary superstitions in contemporary as well as mediaeval societies and in no less a man than the longtime chief game warden of Uganda, Captain Pitman, who described

man-eating as a "taint in the blood". He believed that primitive man had taught this cruel beast to respect the human race and that vigilance was essential to maintain man's ascendancy or else the lions would regain their ancestral mastery of man!

When the man-eaters in Ankole were given international publicity in 1956 it was this sort of fantasy as well as sheer bravado that lay behind the letters from would-be lion killers which flooded the Uganda Game Department Headquarters.

It is very likely that more lions are the victims of human mythology than are ever killed in defence of man or his stock. Lion trophies not only serve the psyche and impart social status but various parts of the animal have been held from the earliest times to have powerful medicinal and magical effects. Conrad Gesner, a physician in Zurich, wrote in 1563:

> "If lion's blood, dried and powdered, is sprinkled on a cancer, it will cure it. Lion's fat is a most precious drug for carbuncles, swollen glands and other hard growths. If mixed with other ointments and rose-oil, it will make blemishes and spots on the face disappear. Eating his heart is supposed to be good against the four-days' cold disease, and his liver pickled and the liquid drunk, alleviates pains in the liver."

Until very recently some traditional Baganda believed that the apparent immunity of most Europeans from magical and other influences could be acquired by eating the umbilical cone on the lion's belly and that this is the lion's own most powerful fetish. Lion fat is believed to join dislocated bones and be a cure for poliomyelitis. Mixed with powdered python vertebrae it heals backache. If the heart is eaten this is thought to impart an imposing dignity upon the eater and will earn him the respect of his fellows. Treated differently it will cure heart disease. Lion-claw fetishes grab every opportunity and are especially sought after by business-men and farmers. Finally, because a man's strength fails and his *Muzimu* or ancestral spirits become helpless before a lion's bristling mane, its hairs are an essential ingredient for smoking the *Kigalanga*, a magical invocation of the spirits' help in overcoming obstacles and achieving desires.

For every lion that lives free there must be space and herds of large animals to support it, so lions do indeed symbolize the world in its primitive

state no less for contemporary conservationists than for the ancient followers of Cybele.

Modern investigations of the lion's biology take place within an evolutionary perspective and this must fundamentally alter our vision of the lion. I have contrasted this viewpoint with tales of myth and fantasy because a portrait of the lion is incomplete without some acknowledgement that over the centuries this animal, more than any other, has been the projection of so many human hopes and fears.

Cheetah (Acinonyx jubatus)

Family Felidae
Order Carnivora
Local names
Duma (Kiswahili), Rumu lititu (Kichagga), Liteeli (Luhya), Kibau (Kikuyu), Ngaku (Kikamba), Liwindi (Lwo), Sumelil (Kalenjin), Arara (Ateso), Andarafes (Kiliangulu), Harmaad (Somali)

Measurements
head and body
130 (112—150) cm
height
78 (70—90) cm
tail
75 (60—80) cm
weight
50 (35—65) kg
(Males weight approximately 10 kg more than females)

Cheetah
(Acinonyx jubatus)

The cheetah's name derives from an Indian word meaning "the spotted one" and it is in India and the plains of southern Asia that early civilizations first came into intimate contact with this animal: a silver vase found at Maikop in the Caucasus is decorated with the representation of a cheetah wearing a collar; the burial mound in which this vase was found has been dated 2300 B.C., which points to a very ancient association between humans and cheetahs.

One can only guess at how such an association began, but cheetahs are perhaps more frequently robbed of their kills than other predators so need to compensate by being extraordinarily effective and frequent killers. Long before the Maikop culture early hunters were likely to have joined other scavenging carnivores in robbing cheetahs of their kills. People living in this way would not have tamed cheetahs, but in favourable localities one can imagine that the dividends of fresh meat would have sharpened human

awareness of the cheetah's habits and behaviour. The relative timidity of cheetahs and their diurnal habits would have been especially appreciated by human scavengers as would their use of relatively open country. Wherever both predators exploited concentrated populations of gazelles and other small ungulates one can be reasonably certain that our hunting scavenging ancestors were well acquainted with the cheetah and its habits. Wherever there have been prey populations to support them, scavenging societies have managed to persist side by side with a variety of post-neolithic cultures. The techniques of the hunters have been readily borrowed or adapted by aristocrats in search of recreation so that the early management of cheetahs that is implied by the Maikop vase might have been founded upon an already ancient familiarity between men and cheetahs.

The Scythians and Assyrians as well as the Ancient Egyptians and Indian civilisations have all left evidence of the taming of cheetahs. In Italy, cheetahs were coursed during the fifth century as well as the early Renaissance. The presence of 1,000 cheetahs in the stables of Akbar the Great (Ali, 1927) illustrates how widespread and abundant cheetahs (and their prey populations) must have been in the subcontinent during the sixteenth century.

Cheetahs were hardly ever bred or even hand-reared and wild populations evidently yielded considerable numbers of weaned or adult animals into captivity. Until very recently cheetahs were captured and trained according to ancient techniques that exploited some of the animals' peculiar characteristics.

Cheetahs can run up to 112 km per hour (Bourlière, 1964) but are exhausted after a few hundred metres. Mounted riders could therefore tire and capture cheetahs very quickly. Once caught the first act was to slip a hood over the animal's eyes. The use of this simple device (which is shown in a famous painting of a cheetah by George Stubbs) represents the trainer's recognition of the primacy of vision in a cheetah's life, which orients its escape, defence and hunting by means of this sense. Hand-feeding returned the hooded animal to a dependence on its human keeper that simulated that of cubhood and was heightened by sightlessness and exposure to strange smells and sounds. Thereafter the cheetah graduated from darkened rooms to controlled hunts.

Like the other spotted cats this species throws up the occasional mutant with peculiar colouring or markings; light brown unspotted individuals, melanistic and white with bluish spots and blotched individuals have all been recorded. Several examples of the latter originating from Rhodesia and Botswana were once described as a separate species, *Acinonyx rex*. It is doubtful whether this species can be meaningfully subdivided even into races despite its far-flung and increasingly fragmented range. Once found all over the more open parts of Africa and from Syria and Arabia to the Kazak steppes and the Indian plains, it has retreated as gazelle populations have declined. Pastures suited to gazelles can often support sheep, and the principal reason for the cheetah's decline has been the steady expansion of sheep herding because, as their natural prey had been supplanted, cheetahs started to kill the sheep precipitating a confrontation that has been won by the shepherds.

Cheetah mutant with marbled spots

Any large population of small or medium-small ungulates is likely to

Overall ranges of cheetahs preferred prey spp

Gazella thomsoni

Gazella granti and *Lithocranius*

Aepyceros melampus

Acinonyx jubatus

Present range
(very rare in western and southern areas)

Estimated former range

support cheetahs if their habitat is not too broken and the vegetation not too dense. In fact, patchy cover helps cheetahs to approach their prey close enough to rush it, whereas completely open plains often allow the quarry too much of a head start. On the other hand, if the ground is too uneven and heavily bushed, the cheetah's rush is impeded. I have seen, for instance, a cheetah come over a hillock on the heels of a fleeing impala and skid on to its back as it tried to avoid an obstacle, betraying that its powers of manoeuvre were inferior to those of the impala.

In East Africa, the cheetah's overall distribution coincides with that of the gazelles and to the south with some of the denser populations of impala. Thus Schaller (1972b) records Thomson's gazelles comprising 91% of cheetah kills recorded on Serengeti, while Pienaar (1969) recorded 68% impala out of 1,092 kills in the Kruger Park. However, they also take a variety of other species; oribi, reedbuck, dik-dik, duiker, young warthogs and the young of various larger antelopes are commonly eaten, while jackals, porcupines, *Orycteropus* and even various large ungulates, including young giraffes and buffaloes have also been recorded. Large prey is only tackled by several cheetah hunting together: the solitary hunter seldom tackles any animal weighing more than about 60 kg.

Cheetahs often appear to choose an individual prey animal before embarking on a chase and they can sometimes be seen on a termitary, tree or other eminence watching a herd attentively before beginning a stalk. Occasionally they will wait in ambush for a herd moving in their direction and

will then rush from very close quarters. Some species of plains ungulates can be approached openly and in these circumstances cheetahs may trot to within 50 metres before launching their high speed attack. In heavily grassed country, cheetahs are particularly helpless while the grass is long, yet even when there have been severe fires, the cheetah's approach may still be difficult because the ungulates appear to have a greater fleeing distance than those habitually living in the open and this may be in excess of the cheetah's striking range. These factors might help to discourage cheetahs from occupying long grass areas. If a herd happens to remain in tight formation when a cheetah rushes it, a kill is unlikely because of the difficulty of selecting an individual victim. The scarcity of zebras in cheetahs' kills may be a result of this. It is also important that the prey should flee. Schaller (1972b) remarked that stationary territorial gazelles may be passed by a hunting cheetah and any antelope or pig standing its ground is also unlikely to be molested. The cheetah painted by Stubbs was presented to George III and was ceremoniously released after a red deer in Woodstock Park to display its hunting prowess to the assembled nobility. However, the stag did not behave as it should and turning on its attacker tossed it high into the air, after which the cheetah absolutely refused to hunt.

In captivity, cheetahs will often charge the fence and stampede ungulates in the neighbouring pens; at Entebbe Zoo the cheetahs persisted in this behaviour long after the zebras, ostriches and antelopes had become habituated and no longer fled when charged. Causing a panic, scattering or stampede would seem to be an integral part of the cheetah's hunting technique as a fleeing animal's balance is very easily upset and the cheetah can quickly attain a stranglehold during the few seconds in which the animal is lying on its back or side. The cheetah pins its prey down at the base of the neck, after twisting the head round so that it can clamp the throat between its jaws while its own body lies facing the prey's back, thus avoiding the flailing

Cheetah strangling prey (from photograph)

legs of the suffocating beast. Because the cheetah's canines are rather short, they only just pierce the skin and the prey is killed by pressure closing off its air supply rather than through wounding. When the prey is very young or weak the cheetah may simply hold the muzzle in its mouth and suffocate it that way. The initial unbalancing of the animal may be achieved in several different ways. When the chase is really fast it is probably easiest for the cheetah to trip the animal up by hooking one of its legs from under it, and this technique has actually been filmed. If the prey is moving more slowly or standing, the cheetah has to rear up, hook into a flank or on the back and yank backwards, the asymmetric pull causing the animal to fall on its side. As the cheetah's toe claws are only moderately curved and are not flexible, the cheetah depends upon its specialized dew claws to hook its prey off balance. This reliance was well understood by Indian huntsmen that coursed cheetahs after gazelles.

> "Cheetahs with blunted dew claws were not able to control full-sized black buck as effectively as those that possessed sharp undamaged ones. We have found therefore that the dew claw is very important to the cheetah and he can also inflict a severe wound with it. Sometimes it is solely by means of the dew claws that the black buck is secured in the chase." (Burton, 1952)

Because females have to rear families, they are probably the most frequent and well practised killers and it has been noticed that within small groups of cheetahs, particular adult females frequently take the lead in catching and killing. After the prey has been suffocated the killer often continues to rest for a while but cheetahs appear to feed rather more rapidly than other cats, a trait that may have been adapted to avoid losing the prey to other predators. Gnawing with the carnassial teeth, the cheetah cuts open the skin on the abdomen; the larger muscle masses on the limbs, back and neck are generally eaten first. An individual cheetah can consume 14 kg at a go and groups of four have been seen to finish an impala carcass in just over fifteen minutes. Bones and skin are usually rejected and sometimes the intestines also. When the latter are eaten, the contents may be squeezed out by the teeth as the gut is sucked into the mouth and throat. A mother making a kill on her own has been known to scratch earth or grass over the partially eaten or untouched carcass and return later with her cubs, but this behaviour is evidently much rarer than in other cats and many observers have asserted flatly that cheetahs never return to their kills.

The degree of success enjoyed by cheetahs is evidently very variable. In the Nairobi Park, McLaughlin (1970) found that 37% of all chases were successful but where the prey were juveniles the chance of being caught rose to 76% and in fact juvenile ungulates accounted for over half the cheetahs' prey in this park, in spite of representing only about 20% of the ungulate population. Nairobi cheetahs kill impala most frequently, followed by Grant's and then Thomson's gazelles. McLaughlin reckoned an average of one kill a day but solitary animals, particularly males, may kill only once in two to five days. Schaller (1972) estimated that a mother with cubs killed an average of 300 animals a year and solitary animals half this amount; 60% of the Serengeti records were of gazelles and about two-thirds of these

were fawns. On the basis of these figures he calculated a biomass representing 8·8 kg a day, of which an average of 4—5·3 kg of meat were eaten.

Hunting is generally conducted in the two or three hours after dawn or before dusk and both the heat of the day and the night are generally spent in concealment or resting. While resting, the narrow deep body lies on its side and only the head is raised from time to time, eyes cresting the surface of the grass. This posture and the conformation of the head with its raised eyes and lowered ears are well adapted to make the cheetah very difficult to see.

McLaughlin noted that males were most mobile, travelling on average about twice the distance travelled by a female and her family, the latter living within a restricted home range and covering about 3·7 km a day to the males' 7·1. The latter are also more willing to continue moving after dark, although several observers have noted cheetahs becoming nervous if darkness found them still feeding or in an exposed situation. Most sightings of cheetahs are in the morning or evening when they are on the move hunting, and even the sharpest-eyed observer is likely to miss seeing cheetahs if they are deliberately evading detection by lying in grass clumps or thickets. This evasiveness and the regular changing of lying-up spots and hunting grounds have probably contributed to the belief that cheetahs are very rare, yet this cryptic behaviour is an important strategy in their survival amidst numerous competing predators, particularly hyaenas, lions, dogs, humans and, in some areas, leopards, all of which have been recorded killing cheetahs. Records of lions killing cheetahs are especially numerous and the roar of a lion nearby is often sufficient to make a cheetah flee, take cover and freeze, change course, or even abandon a meal and the sight of one always precipitates instant flight.

The ability to "disappear" in the open grassy country and the animal's timidity are allied to physical defencelessness. The cheetah's hunting and killing techniques are so dependent on the fleeing response of its prey that they cannot be adapted to defence. As a result cheetahs escape confrontations by hiding or else they may attempt a bluff threat, which appears to be a somewhat more extreme form of intraspecific threat. The teeth are exposed in a wide-mouthed snarl and the body is bunched while the eyes glare upwards from the lowered head. Sudden forward leaps or even short charges are accompanied by a hard synchronized thump with the forepaws, similar to the striking action used against small prey like rodents or game birds: but threats have not been seen to develop into a serious attack, although a fleeing jackal has been reported to have been killed. Nonetheless, these threats are certainly effective as two cheetahs have been seen to repulse eight hyaenas. The fact that this kill had been made in the early morning might have influenced its outcome, for the reverse situation, hyaenas chasing a cheetah, was seen at night on Serengeti. Threats are accompanied by moaning or, at higher intensities, by hissing and very occasionally by a growl. If the animal lunges it may make a short yap as it snaps its teeth.

Cheetahs have an extensive repertoire of sounds. The most striking call is an explosive yelp, in which the animal's chest and head jerk with the effort. This call has a great carrying power and McLaughlin (1970) could hear it from a distance of 2 km. It is essentially a contact call and is most commonly uttered by a separated mother, juveniles or sibling companions but adult males also yelp. ~~Its~~ timbre can be likened to the spurfowl's croak and at a

lower volume to a passerine's chirrup, but the call appears to have a wide range of intensity and be subject to considerable variation, in which the individual's "signature" may play a not inconsiderable part. Juveniles at a kill make a whirring sound which may be equivalent to the warning growl of other felids, which can subside into a high-pitched rasp or rise to a ferocious squeal which generally signifies active fighting. Chirping accompanies any excited meeting between cheetahs that know one another, at a kill, around an oestrous female or at a scenting post and it is frequently interspersed with a rather metallic purring.

Purring accompanies play and various friendly encounters in which cheeks are rubbed together and much mutual sniffing and face-licking may take place but no body-leaning or side rubbing as is commonly seen in other cats. Purring is quite distinct from a curious humming noise which is occasionally heard from captives anticipating food. Adamson (1972) heard a cub make this noise as it began to stalk. She also describes a "nyam, nyam, nyam" associated with eating. Several calls have only been heard in the context of a mother and her young. Eaton (1970b) described cubs grouping and keeping still in response to a short low-pitched sound from the mother; cubs will even stay and watch the mother feeding until she releases them from their immobility by calling them: releasing calls are the loud yelp (from a distance) or a call Adamson (1969) describes as "ihn, ihn, ihn", which is used to call up hidden or lost young, or else a sharp "prr prr", which is specifically associated with movement and elicits close following of the mother. Very young cubs in a hiding place may respond to disturbance or to the arrival of the mother with a sound like the breaking of a stick. Although moaning is heard in threat a rather bleat-like moan denotes distress and is made by a pursued or lost animal.

The most lasting and conspicuous social bonds are between a mother and her cubs and between siblings. Also there have been repeated observations of several adult males together but of unknown relationship (see Foster and Kearney, 1967) and the latter grouping often results in the hunting and killing of prey that is larger than average.

The most thorough study of the cheetah's social life and behaviour to date is that of McLaughlin (1970) in the Nairobi National Park. Here he was able to follow three distinct and independent groups numbering eleven animals altogether. He encountered 21 other cheetahs in the park, all of which were transient. The total range of one family group was estimated at 82 sq km and another at 76 sq km. These figures are probably a fair average for a locality with reasonably abundant prey but it is obvious that food resources are an important determinant of the extent of the cheetah's range. Schaller (1972b) noted a mother and her cubs remaining within ten sq km for about one-and-a-half months and Adamson's partly hand-fed but free-ranging female lived within a range of about 56 sq km. The large proportion of transients recorded by McLaughlin illustrate how mobile most cheetahs are even in areas with abundant prey. The large-scale movements of gazelle populations on Serengeti are followed by cheetahs and might result in different seasonal ranges, but even Adamson's cheetahs, with every inducement to remain in a small locality, chose to change their lying-up spots and hunting grounds every few days or even daily. Very young cubs slow down this con-

tinuous circulation but even so the mother changes her shelter regularly, if only for a few hundred metres or so. Both McLaughlin and Adamson noted extensive overlaps of home range among adults in spite of this. An individual's or family's favourite area was very seldom intruded into for very long, even by adult offspring of a former litter.

The favourite area always contains a number of elevated points which are regularly marked by the resident cheetahs with excreta. These marked trees, stumps, termitaries, hillocks, rocks or banks are focal points for any cheetah. Those living within the area revisit them regularly, males and females depositing dung and the former also squirting urine. Transients also tend to go from one vantage point to another and often add their deposits after sniffing at what was already there. It looks as if viewpoints also provide natural foci for all types of indirect social contact, for urine and dung can presumably carry the signature of a known individual as well as indicate a stranger's sex and condition. These places are certainly social landmarks for cheetahs but they have been variously described as meeting points or rendezvous, territorial marking posts and latrines. The Indian huntsmen knew these places well and used to trap cheetahs when they revisited such landmarks (Sterndale in Hanström, 1949). A cheetah's reaction to the message contained in a urine-sprayed tussock or dung on a termitary must obviously vary according to its own sex and status, but evasion is by no means the only reaction as some authors have asserted.

McLaughlin stressed that a scent mark may excite curiosity in the first place rather than avoidance and Adamson described her family of cheetahs often choosing to play around these places. She also noticed that previously attractive viewpoints were abandoned after the group dispersed. Deliberate chasing away of female members of the former litter was seen and there was a readjustment of home range; with the arrival of a new litter there was a quite different choice of trees and termitaries from those that had been frequented with the previous one. This suggests that the female's deposits are one manifestation of a particular family's link with its environment (the tendency to play at such spots implies a heightened sense of security) and the link dissolves with the dispersal of that family and requires to be built up anew with another litter. The fact that female members of an older litter are no longer tolerated can only reinforce the obsolescence of the landmarks associated with them.

Adult females are the least tolerant of all cheetah classes and are very seldom seen together. Furthermore, the mother of a litter is the most sedentary of all classes and her marking of the favourite viewpoints in her range probably repels other females. Adamson (1969) knew and followed four related females over a period of several years and they were effectively territorial in that none of them seemed to intrude into one another's hunting grounds, while males, on the other hand, appeared to roam around at random. Mrs Adamson was frequently threatened by a particularly aggressive subadult female when on the cheetah's home ground, but this animal lost all trace of aggression if she accompanied her hand-reared mother on visits to Mrs Adamson's camp. This and other young females exhibited an altogether more defensive disposition than male cubs, a trait that was apparent at an early age. An example of female intolerance was provided by this mother's bolting, together with

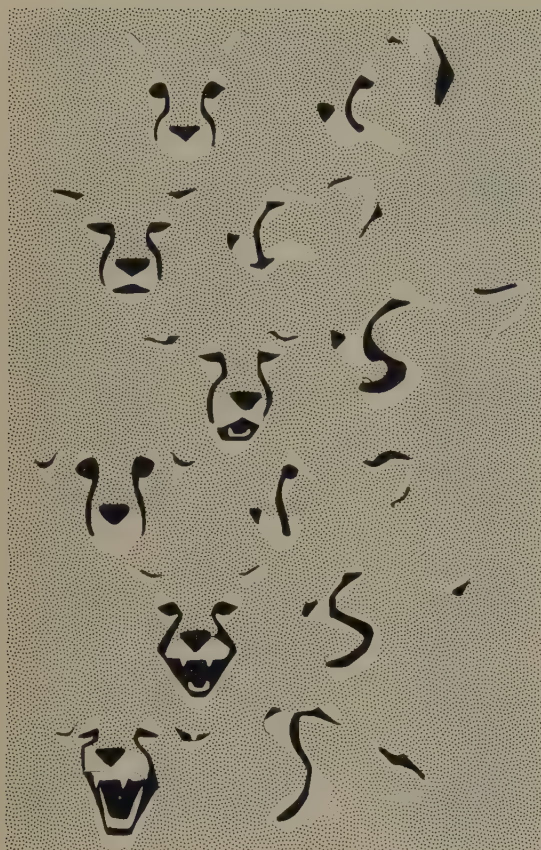
her cubs, at the sight of an adult daughter. However, having hidden her young the mother made an aggressive come-back.

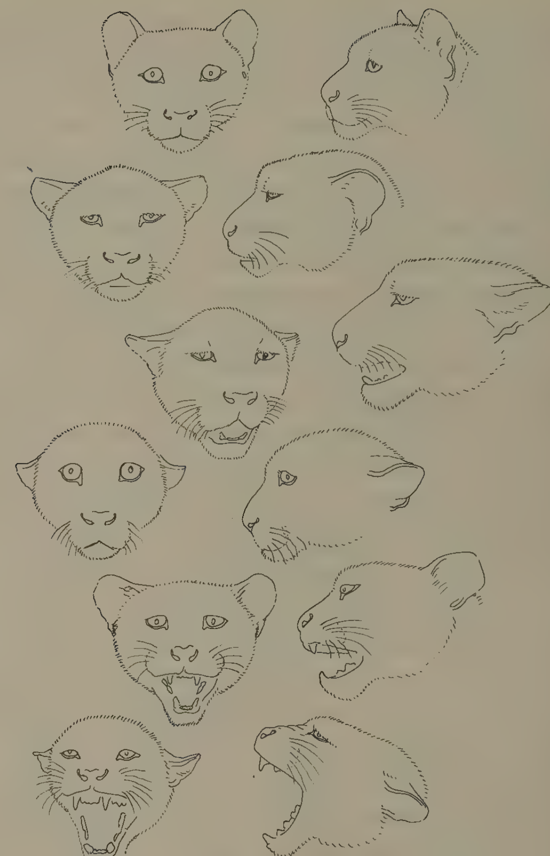
McLaughlin often saw males together but never all-female groups; he thought mixed groups represented recently independent litter-mates and Moss (1976) recorded that one young male in the Nairobi Park joined up with two others when he left his mother. In a captive colony in America, Eaton (1972) introduced a stuffed cheetah dummy. Males did not attack this, whereas females gave every sign of trying to kill the intruder.

The results of a questionnaire survey covering nearly 1,000 sightings were reported by Graham and Parker (1965) (in Graham, 1966). Nearly half these were of single adults and 31·6% were of two and 11·8% of three; only 3·1% were of groups containing over five adults. Again, these authors remarked on the absence of female groups and noted that females do not even travel very often with males. McLaughlin frequently saw males make attacks on family groups, but given the extended and aggressive nature of courtship it is likely that these attacks were a manifestation of sexual behaviour (see below).

Males occasionally attack other males and Alan Root has filmed an occasion where two males killed a third. On two other occasions a fatal fight has been seen to break out over a kill. However, Stevenson-Hamilton (1954b) reported a male killed in a fight over a female and captive males often fight fiercely over an oestrous female. Eaton (1973) regarded the fights he observed in a zoo pen as highly ritualized in nature. An interesting interaction between two males in Kidepo National Park was seen by Ross (personal communication). A solitary adult male lying near a small hillock was approached by a second male, which announced its arrival with yaps interspersed with purring. The first male flattened itself as though to hide but the second cheetah could nonetheless see him. However, he continued to move in an agitated manner, still yapping over the top of the hillock, where he was out of sight of the first cheetah, which then moved over and sheltered under a bush. Some hours later the situation appeared not to have changed; the second cheetah was still near the top of the hillock, trotting around there, yapping and he was twice seen to smell and spray a tree trunk. Suddenly he started to run and Ross thought he was after some nearby gazelle but he broke right, charged the first cheetah and struck him with his forepaw. He then moved off into the dusk, still yapping and purring. Although the cuff was the only sign of direct confrontation, it is tempting to believe that the second cheetah displaced the first and that the calling, posturing and urine spraying on the hill top represented a dominance display. Although too little is known about cheetah behaviour in general and the nature of inter-male relationships in particular, to be able to interpret such incidents with any certainty, there are close resemblances with sexual behaviour which will be discussed shortly.

While families tend to be the most restricted in range there is also some evidence that some males or even male groups may be more resident than others (McLaughlin, 1970; Schaller, 1972b). Cheetahs may resemble the other cats in that young and inexperienced males tend to be forced into a more nomadic existence by the intolerance of older cats. As they wander over a large area males probably meet many other individuals. Although these encounters may be sporadic it is possible that loose hierarchies emerge between individuals and groups as well as within groups. Adamson (1972) saw





clear evidence of a hierarchy between members of both sexes within litters but she also saw changes in status.

Like other cats, cheetahs signify submission by falling on their backs and presenting their white underparts to the aggressor. They moan at the same time and this seems to inhibit attack. At greater distances a threatening advance may be deflected by the submissive animal sitting down sharply on its haunches and looking away with its mouth closed and somewhat pursed. This response has even been seen when large or aggressive animals, instead of running away, turned to face a charging cheetah. The facial expression of a submissive cheetah is peculiarly pinched because the black margins of the mouth are hidden. In confident or aggressive expressions the black tear stripe and lips are joined together in an emphatic geometric figure. Eaton (1970b) suggested that the stripe might be an anti-glare device but a more plausible explanation is that it serves to emphasize expression. Expressions are primarily directed at other cheetahs but snarls and snaps are part of the animal's bluff in defence of its prey and so a spectacular snarl might also be advantageous against a competitor.

There is no ruff to enlarge the face mask as there is on many other cats, on the contrary, the overall pattern of spots continues past the ears so that at a distance the head becomes almost as difficult to see as the body. Camouflage is useful to the cheetah both as a hunter and as the first line of defence for a persecuted subordinate of more aggressive carnivores and scavengers. It is

only at very close quarters that the mouth, muzzle and eyes emerge from the spotted matrix, and the black markings that surround and link these organs of expression certainly serve to bring them into great prominence once the animal is close enough to be actively responding to the presence of another animal. Although the back of the ears are also boldly patterned, these markings only show up well from behind or when the head is lowered in intraspecific threat. The visual role of the black stripe and lip margins is best illustrated by comparing drawings of the animal's expressions with identical outlines in which the black margins have been removed.

In an environment of grass and scattered scrub the cheetah is a very inconspicuous animal and it is only on their elevated viewpoints that cheetahs allow themselves to become conspicuous and assume what might be called display stances; cheetahs rely mainly on sound, however, to communicate with one another over a distance.

Amongst the litters watched by Mrs Adamson there was one containing a female and two male cubs; when the males matured at fifteen months they engaged in much homosexual mounting as well as attempting to copulate with their sister, and copulations were interspersed with metallic purring, urine squirting around a fallen tree, circular chasing and spanking at one another's legs. There are numerous observations of several males copulating with a female in turn. On average the female's oestrus lasts about two weeks and is preceded and succeeded by periods of increasing and diminishing receptivity, during which time the scent of her vaginal discharge and frequent urine squirts may be responsible for the males' convergence. Akbar, The Mogul Emperor, recorded trapping six male cheetahs which were apparently in pursuit of a female in season (Ali, 1927).

The males in a captive group watched by Herdman (1972) fought one another in order to remain closest to the female, and a dominant male emerged. As a female came into oestrus Herdman noticed a marked increase in the frequency with which males sprayed urine on to prominent landmarks or tussocks. Urine is also directed on to debris piled together by scratching by the hindlegs. Clawing, which is important in most felid species, seems to be mainly associated with courtship in cheetahs and Schaller (1972b) saw a female raking her front claws past the face of an advancing suitor. She would roll in front of him and then dash away only to approach again. Although males are larger and more powerfully built, females are usually the more aggressive sex and exhibit submissive behaviour only during oestrus. Males are frequently aggressive towards an oestrous female, knocking her over and slapping at her, even biting at her flanks or hindquarters. The female often attempts to hide under thorn bushes, but impulses appear to alternate and she emerges only to be subjugated again. Mutual mouth to mouth licking and grooming of the chin is common in siblings and also occurs between adults during resting periods in between bouts of harassment or copulation, but interest in one another wanes as oestrus declines and the males eventually desert the female completely.

The gestation period lasts 90—95 days and, although there is a record of eight cubs in one litter (Graham, 1966), the usual number is three or four. They are born and hidden in a well-concealed retreat under a bush.

(Mrs Adamson's Pippa always chose the wait-a-bit thorn, *Acacia mellifera*, to hide her young.)

There seems to be an extended birth season in tropical East Africa between January and August with the majority of births between March and June. Late litters are occasionally burnt to death in the grass fires that start in June or July. Indeed, the timing of births may have been influenced by this hazard. There is no evidence to suggest that females are unable to feed themselves or their young at any time of the year, but Cade (1966) describes three well-grown cubs that had lost their mother wandering into a Kenya township in the last stages of starvation, illustrating how vulnerable and helpless young or inexperienced juveniles are. However, it seems very unlikely that the vicissitudes of large cubs and subadults could influence the timing of a birth season as has been suggested by some authors.

At birth the young are unco-ordinated and blind but they can turn their heads towards a disturbance and spit explosively. They weigh about 150—300 g and appear to be dirty white above and black below; before long the spots begin to assert themselves as the underparts lighten but the long mantle of greyish fawn fur covering the cubs' back, nape and crown disappears more slowly. Although a cub is tawny and spotted almost all over by the time it is three months old, the last traces of a crest are still present when a cub becomes independent at the age of about fifteen months. Various suggestions have been made about the meaning of this pale woolly mantle: that it acts as a thermostatic umbrella against rain and the radiation of the

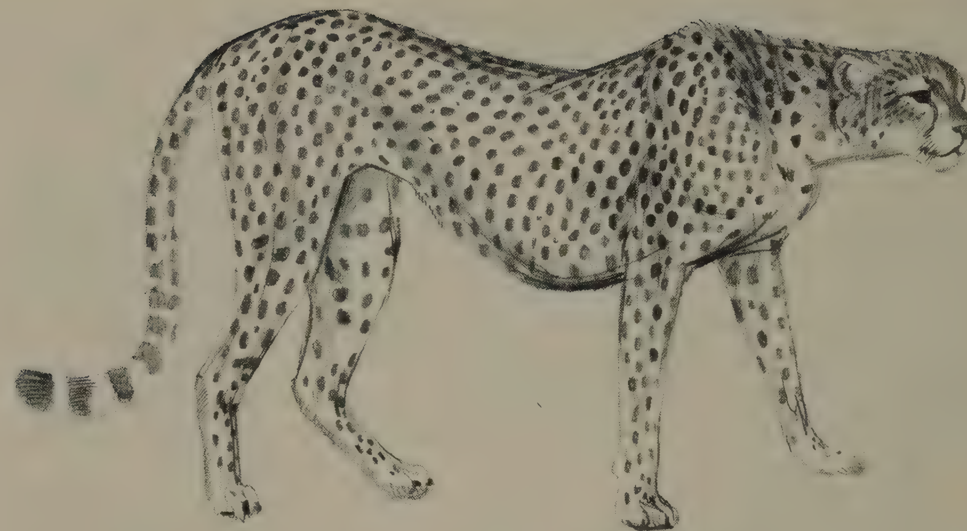
sun and that it is a camouflage imitating the dry dead grass. While it is likely that both these functions are served, there is also a third possibility. Intraspecific appeasement behaviour, exposing the belly, starts rather late among cheetahs, when they are fully mobile and with semi-adult colouring. Very young cubs respond to an alarm by freezing and this immobile position leaves the young's back exposed. Males have occasionally been recorded killing cubs, but such a response could perhaps be inhibited by a reversal of colouring. If it could be shown that aggression was inhibited by the sight of white fluffy fur in adult conflicts, the light fur on the baby cheetah's back might

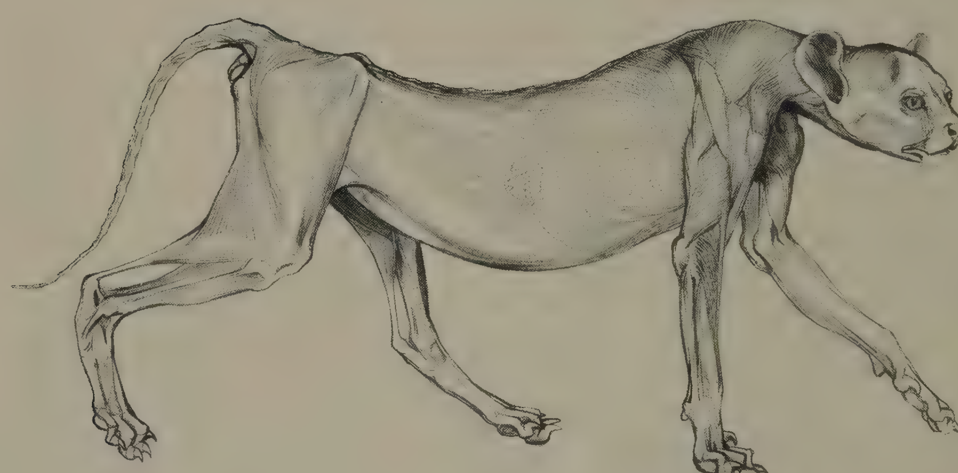
then be shown to have a survival value. It has already been mentioned how a mother fled and hid her young cubs from her adult daughter. This mother would decoy anyone attempting to follow her to her recently-born litter by going in the opposite direction and then doubling back. Her evasion technique was to sit quite still until she could slip away unnoticed. All observers have stressed how cautious and patient females are when visiting their hidden young. This makes Mrs Adamson's report on the mother's lack of concern for elephants all the more astonishing (Adamson, 1972). She suggested that the mother deliberately kept her young close to a herd of elephants for the security they engendered and she describes the cubs being enveloped in dust churned up by an elephant's feet while it fed on the branches of the bush beneath which the cubs were sheltering. Shelters are sometimes moved daily and Adamson recorded twenty-one moves in six weeks and a maximum stay in one spot of twelve days.

The young open their eyes at four to eleven days and teeth break through the gums at about three weeks. Florio and Spinelli (1967) record a captive mother regurgitating meat in front of the cubs when they were eighteen days old, but such behaviour has not been seen in the wild. The cubs can generally walk well at three weeks but do not accompany the mother until they are about six weeks old, keeping very close to her and responding quickly to her calls; from this time onwards they are normally inseparable from the mother and during the first three months the young are an obstacle to successful hunting. The mother, however, appears to be able to inhibit following by a short low-pitched noise and their immobility is released by another call. At other times Mrs Adamson's mother cheetah was seen to induce playing cubs to follow her by dashing round them in circles, whereupon they chased her and she then led them off. The same animal appeared to solicit her human companion for a walk by deliberate jerking of the head.

The mother plays with her young but the most intensive and continuous play is amongst siblings. Elements of hunting behaviour are unmistakeable with chasing, batting with forepaws, leaping into the air and spinning round and round an injured prey animal. Perhaps the readiness of captives to retrieve balls and their trembling with excitement in anticipation of the next throw is part of this early practice of hunting skills. Play very often takes place on a favourite tree or other elevated landmark and may involve mock fighting and chasing as well as invitations to tugging contests and attempts to dislodge one another. Much mutual mouth licking is characteristic of resting spells in between bouts of activity and before the young leave their mother elements of sexual behaviour also appear. Hierarchies are apparent in play but these first appear as infants struggle at the mother's nipples and, according to Adamson, the status of a sibling may change.

The time of weaning varies as the female may cease to lactate between fourteen and twenty-four weeks but growth is very rapid. They are half adult size at six months and at eight months lose the last of their deciduous teeth, the canines. At about this time the cubs are allowed to make their first clumsy attempts at stalking and catching and if fawns are around these efforts may be successful. Prior to this the mother catches all the food, although she may carry living young animals to the cubs, which attempt to strangle dead





or dying prey from an early age. Between twelve and fourteen months the young start making successful kills on their own.

The heaviest mortality occurs when the young start to follow the mother and McLaughlin estimated that a litter average of 4·2 cubs at birth was down to 2·5 by the time the young are independent. A female can conceive at 21—22 months and thereafter the average interval between giving birth and conceiving is about eighteen months (Schaller, 1972b), although Spinelli and Spinelli (1968) noted a captive female coming into oestrus four months after giving birth and Adamson's female mated a few weeks after a new litter.

Schaller (1972b) points out that the population turnover is higher than that of lions or leopards and he remarks that unknown factors keep the Serengeti population depressed and seemingly stable at a very low level, his estimate of density standing at about one cheetah per 260 sq km, whereas McLaughlin's estimate for the Nairobi Park was about one per 5 sq km. Such disparities make any attempt at estimating total populations virtually

impossible, but popular interest in the cheetah has encouraged some conservationists to guess figures. Meyers (1975) suggested 15,000 for the whole continent while Eaton (1971) published a figure of 2,000. The latter is lower than a realistic estimate for Kenya alone, where cheetahs range at variable and unknown densities.

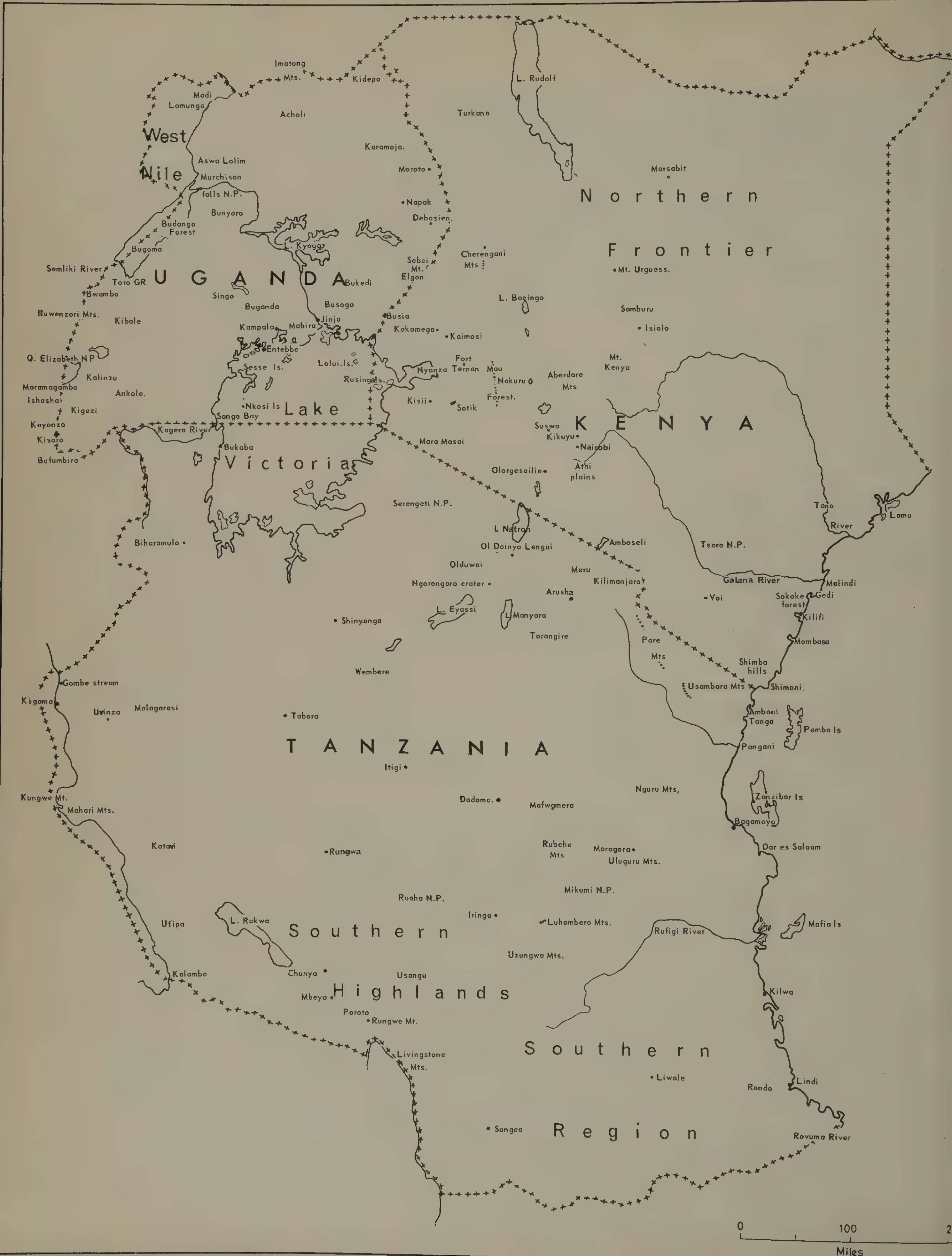
Limiting factors on cheetah populations are very poorly understood. The roles of competition, of the physical environment, of fires and of prey populations have been mentioned earlier. Diseases known to affect cheetahs are anthrax (Pienaar, 1969), tick fever, *Babesia felis*, feline enteritis (Murray, 1967) and a variety of parasites may accumulate in a malnourished animal. Loveridge (1933) records a sick animal being infested with *Ctenocephalus* fleas, ticks, hippoboscid flies and the larvae of *Spharganum*, which he thought might have been collected through eating frogs or fish. Experiments have failed to induce tse-tse flies to feed on cheetahs and they have not been recorded to suffer from trypanosomiasis, and their scarcity in the miombo woodlands is probably due to a shortage of suitable prey. The longest life record for captivity is fifteen years and seven months but the average life of captives is five years and two months. (Van der Werken, 1968.)

Interest in conservation has highlighted the poor breeding record of cheetahs in most zoos. This reluctance to breed has been recognized and discussed for many years; as wild males only approach a female when she is in season, the zoo habit of keeping a pair in permanent close confinement may inhibit mating. Whipsnade Park in England has had the greatest success to date. Eaton (1973, 1974) has discussed the problems of breeding in captivity. In this connexion it is interesting that the seventeenth century Moghul Emperor Jehangir Khan had this to say:

> "It is an established fact that cheetahs in unaccustomed places do not pair off with a female and my revered father (Akbar) once collected together 1,000 cheetahs. He was very desirous that they should pair, but this in no way came off. At this time a male cheetah, having slipped its collar, went to a female and paired with it and after two and a half months three young ones were born and grew up. This has been recorded because it appears strange." (Ali, 1927)

Ghenghis Khan, Akbar and Jehangir were all avid coursers of the cheetah as was Charlemagne. For these royal patrons the cheetah was perhaps the vehicle for projections of grace, speed and superiority as well as the provider of thrills of the chase (now widely satisfied by greyhounds and mechanical contrivances). The Ancient Egyptians endowed the cheetah with the spirit of courage, while a contemporary projection is of the elusive grace of a declining wilderness.

Is it the persistence of extraneous human projections or is it the animal's intrinsic elusiveness that has been responsible for the paucity of scientific information on an animal that we have good reason to believe has been handled by men for well over 4,000 years? In any event, the elusive cheetah remains a challenge to the naturalist.



Imatong
Mts.
Kidepo
L. Rudolf
Madi
Lomunga
Acholi
Turkana
West
Nile
Karamoja.
Aswa Lolim
Murchison
falls N.P.
Moroto
Marsabit
Northern
Napak
Bunyoro
Debasien
Budongo
Forest
L. Kyoga
Bugoma
Cherengani
Mts
Frontier
Semliki River
Sebei
Mt.
Elgon
Mt. Urguess.
Toro GR
UGANDA
Bukedi
Bwamba
Singo
Buganda
Busoga
L. Baringo
Samburu
Ruwenzori Mts.
Kibale
Busia
Isiolo
Kampala
Mabira
Jinja
Kakamega
Kaimosi
Entebbe
Mt.
Kenya
Q. Elizabeth NP
Lolui.Is.
Fort
Ternan
Mau
Sesse Is.
Nyanza
Kalinzu
Nakuru
Aberdare
Mts
Rusinga Is.
Maramagambo
Ankole.
Ishasha
Kisii
Forest.
Sotik
Nkosi Is
Lake
Kigezi
Songo Bay
KENYA
Kayonza
Suswa
Kikuyu
Kagera River
Mara Masai
Kisoro
Bukoba
Nairobi
Victoria
Bufumbira
Athi
plains
Olorgesailie
Serengeti N.P.
Tana
River
Lamu
L Natron
Biharamulo
Amboseli
Ol Doinyo Lengai
Tsaro N.P.
Olduwai
Meru
Kilimanjaro
Galana River
Malindi
Ngorongoro crater
Arusha
Voi
Sokoke
forest
Gedi
L. Eyassi
Shinyanga
Manyara
Kilifi
Tarangire
Pare
Mombasa
Mts
Wembere
Shimba
hills
Gombe stream
Usambara Mts
Shimoni
Kigoma
Uvinza
Malagarasi
Tabora
Amboni
Tanga
Pemba Is
TANZANIA
Pangani
Itigi
Kungwe Mt.
Nguru Mts,
Zanzibar Is
Mahari Mts.
Dodoma.
Mafwgmera
Bagamoyo
Katavi
Rungwa
Rubeho
Mts
Morogoro
Uluguru Mts.
Dar es Salaam
Mikumi N.P.
Ruaha N.P.
Ufipa
L. Rukwa
Iringa
Luhombero Mts.
Mafia Is
Southern
Rufigi River
Uzungwa Mts.
Kalambo
Chunya
Usangu
Kilwa
Mbeya
Highlands
Poroto
Rungwe Mt.
Livingstone
Mts.
Southern
Liwale
Lindi
Rondo
Songea
Region
Rovuma River
0
100
Miles

Gazetteer

Abercorn Zambia 8° 50′ S 31° 25′ E
Aberdare Mts C. Kenya 1° 20′—1° 40′ N 36° 40′ E
Acholi N. Uganda
Albert, Lake W. Uganda
Amboni N.E. Tanzania 5° 3′ S 39° 4′ E
Amboseli S. Kenya 2° 40′ S 37° 10′ E
Angola S.W. Africa
Ankasa Forest, Ghana
Ankole S. Uganda
Arusha N. Tanzania 3° 23′ S 36° 43′ E
Aswa-Lolim G.R. 2° 35′ N 31° 45′ E
Athi Plains C. Kenya 1° 30′ S 36° 50′ E
Avakubi Zaire 1° 30′ N 27° 25′ E
Bagamoyo Tanzania Coast 6° 25′ S 38° 54′ E
Baringo Lake 0° 40′ N 36° 5′ E
Biafra W. Africa
Biharamulo N.W. Tanzania 2° 38′ S 31° 19′ E
Botswana Southern Africa
Budongo W. Uganda 1° 45′ N 31° 40′ E
Bufumbira Mts E. Congo W. Uganda
Buganda S. Uganda
Bugoma W. Uganda 1° 20′ N 31° E
Bukedi E. Uganda 0° 40′ N 33° 50′ E
Bukoba N.W. Tanzania 1° 21′ S 31° 48′ E
Bunyoro W. Uganda
Burundi C. Africa
Busia E. Uganda 0° 30′ N 34° 8′ E
Busingiro (see Budongo) W. Uganda
Busoga S.E. Uganda
Bwamba W. Uganda 0° 40′ N 30° E
Cameroons W. Africa
Central African Republic or Congo Brazzaville

Central Refuge E. Congo (Zaire)
Chad Lake W. Africa
Chania River, Mt Kenya, Chandlers Falls N.F.D. Kenya 1° N 37° 45′ E
Cherengani Mts W. Kenya 1° 15′ N 35° 25′ E
Chitau Angola
Chunya S.W. Tanzania 8° 32′ S 33° 25′ E
Comoros Islands Indian Ocean E. of Madagascar
Congo basin C. Africa
Congo River C. Africa
Cross River Nigeria
Dabaga C. Tanzania 8° 7′ S 35° 55′ E
Dar-es-Salaam Tanzania Coast 6° 48′ S 39° 18′ E
Darfur W. Sudan
Debasien, Mt E. Uganda 1° 45′ N 34° 50′ E
Dodoma C. Tanzania 6° 11′ S 35° 45′ E
Dungilia River Southern slopes of Ruwenzori
Dura River W. Uganda 0° 30′ N 30° 25′ E
Echuya Swamp S.W. Uganda 1° 15′ S 29° 45′ E
Edward Lake W. Uganda
Elgon, Mt E. Africa 1° 10′ N 34° 35′ E
El Obeid Sudan
Embu C. Kenya 1° 30′ S 37° 30′ E
Eritrea Red Sea Coast
Ethiopia N.E. Africa
Ethiopian Faunal Region African Continent with Arabia
Eyassi, Lake C. Tanzania 3° 40′ S 35° E
Fayum Egypt
Fernando Po Is W. Africa
Fort Ternan W. Kenya 0° 20′ S 35° 25′ E
Gabon, Gaboon W. Africa
Gambia W. Africa
Garguess or Urguess, Mt (now known as Warges N.F.D. Kenya)
Garissa N.F.D. Kenya 1° 30′ N 39° 40′ E
Gedi Kenya Coast 3° 18′ S 40° E
Ghats "African Ghats" E. Tanzania
Gombe Stream Reserve W. Tanzania 4° 59′ S 30° 57′ E
Greek River S.E. Uganda 1° 28′ N 34° 35′ E
Gregory Rift Eastern Rift Valley, Kenya
Hannington, Lake Kenya 0° 20′ N 36° 5′ E
Haut Ituri N.E. Zaire 2° N 30° 30′ E
Hoggar or Ahaggar Mts Algerian Sahara
Horn of Africa N.E. Africa
Imatong Mts S. Sudan 4° N 32° 50′ E
Impenetrable Forest (now Bwindi) S.W. Uganda 1° 5′ S 29° 40′ E
Iringa S. Tanzania 7° 47′ S 35° 42′ E
Ishasha W. Uganda 0° 48′ S 29° 35′ E
Isiolo G.R. 0° 22′ N 37° 35′ E
Itigi Thicket C. Tanzania 5° 40′ S 34° 30′ E
Ituri E. Congo

Ituri Maniema E. Congo (Zaire)
Ivory Coast West Africa
Jinja S. Uganda 0° 25′ N 33° 15′ E
Jombeni Mts C. Kenya 0° 25′ N 38° E
Kabale W. Uganda 1° 18′ S 30° E
Kadam, Mt E. Uganda 1° 45′ N 34° 40′ E
Kagera River Uganda, Tanzania border
Kaimosi W. Kenya 0° 18′ N 34° 55′ E
Kaiso W. Uganda 1° 35′ N 30° 58′ E
Kakamega W. Kenya 0° 20′ N 34° 45′ E
Kalahari S.W. Africa
Kalinzu W. Uganda 0° 30′ S 30° E
Kampala S. Uganda 0° 20′ N 32° 35′ E
Kanjera Kenya 0° 55′ S 36° 25′ E
Karagwe N.W. Tanzania 1° 15′ S 31° 50′ E
Karamoja E. Uganda
Kasai River Congo basin
Kashasha River Kivu District, Zaire
Katanga Southern Zaire
Katavi Plain W. Tanzania 6° 30′—7′ S 31° E
Kayonza W. Uganda 1° S 29° 35′ E
Kenya Highlands C. Kenya
Kenya, Mt E. Africa 0° 10′ S 37° 25′ E
Kiambu C. Kenya 1° 10′ S 36° 15′ E
Kibale Forest W. Uganda 0° 30′ N 30° 35′ E
Kidepo Valley N. Uganda 3° 50′ N 33° 55′ E
Kigezi W. Uganda 1° S 30° E
Kigogo S.W. Tanzania 8° 37′ S 35° 15′ E
Kigoma W. Tanzania 4° 52′ S 29° 38′ E
Kikuyu C. Kenya 1° 20′ S 36° 40′ E
Kilifi Kenya Coast 3° 40′ S 39° 50′ E
Kilimanjaro N. Tanzania 3° S 38° E
Kilombero River and Valley Tanzania 9° S 36° E to 8° S 37° E
Kilwa Tanzania Coast 8° 45′ S 39° 25′ E
Kinshasha Congo Kinshasha
Kiriandongo N.W. Uganda 1° 50′ N 32° 7′ E
Kiserawe Dar-es-Salaam 6° 53′ S 39° 3′ E
Kisoro W. Uganda 1° 18′ S 29° 40′ E
Kisii W. Kenya 0° 40′ S 34° 45′ E
Kivu, Lake E. Congo
Kivu Province E. Congo
Kungwe, Mt W. Tanzania 6° 8′ S 20° 48′ E
Kyarumba Ruwenzori 0° 10′ N 29° 55′ E
Kyoga, Lake C. Uganda 1°—2° N 33° E
Laetolil near Olduvai N. Tanzania
Lamia River, Bwamba Uganda
Lamu Kenya Coast 2° 20′ S 40° 58′ E
Liberia W. Africa (Limpopo Rivers borders N. Transvaal S. Africa)
Lindi Tanzania Coast 10° S 39° 45′ E

Livingstone Mts S.W. Tanzania
Liwale S.E. Tanzania 9° 47′ S 37° 58′ E
Loita Plains C. Kenya 1° S 35° 35′ E
Lolokwi, Mt N.D.F. Kenya 1° 20′ N 37° 17′ E
Lolui Is. Lake Victoria 0° 10′ S 33° 45′ E
Lomunga G.R. 3° 35′ N 31° 30′ E
Luhombero, Mt C. Tanzania
Lushoto N. Tanzania 4° 47′ S 38° 17′ E
Mabira S. Uganda 0° 30′ N 32° 50′ E
Madehani S.W. Tanzania 9° 20′ S 34° E
Madi N.W. Uganda
Mafia Is. Tanzania Coast
Mafuga Forest Plantation S.W. Uganda 1° 10′ S 29° 45′ E
Mahari Mts W. Tanzania 6° S 30° E
Makerere, Kampala S. Uganda
Malagarasi W. Tanzania 4° 5′ S 29° 30′ E
Malawi C. Africa (also Lake Malawi)
Malindi Kenya Coast 3° 8′ S 40° 10′ E
Manyara, Lake N. Tanzania 3° 30′ S 35° 50′ E
Mara Masai G.R. S.E. Kenya
Maramagambo W. Uganda 0° 30′ S 29° 50′ E
Marsabit N. Kenya 2° 25′ N 38′ E
Masaka S.W. Uganda 0° 20′ S 31° 40′ E
Masindi W. Uganda 1° 45′ N 31° 40′ E
Matanga N. Pemba Is.
Matengo Hills 11° S 34° 50′ E
Matopos Hills Rhodesia
Mau Forest Kenya 35° 35′ S 36° 20′ E
Mauritania Western Sahara
Mawokota S. Uganda 0° 22′ N 32° 22′ E
Mayanja Forest near Kampala
Mbale East Uganda 1° 5′ N 34° 10′ E
Mbeya S.W. Tanzania 8° 54′ S 33° 26′ E
Menengai, Mt 0° 10′ S 36° 5′ E
Meru, Mt Tanzania 3° 15′ S 36° 45′ E
Mgogoni N. Pemba Is.
Mikumi Nat. Park E. Tanzania
Milanje, Mt S. Malawi
Mkulumuzi Caves N.E. Tanzania 5° 3′ S 39° 4′ E
Mombasa Kenya Coast 4° S 39° 35′ E
Momella, Lakes N. Tanzania 3° 12′ S 36° 52′ E
Mongiro Bwamba Uganda
Morogoro E. Tanzania 6° 48′ S 37° 40′ E
Moroto E. Uganda 2° 30′ N 34° 45′ E
Mozambique E. Africa
Moyale N.F.D. Kenya 3° 30′ N 35° 5′ E
Moyovosi River N.W. Tanzania
Mpwapwa C. Tanzania 6° 22′ S 36° 30′ E
Muheza Usambra Mts N. Tanzania

Muko Forest Plantation S.W. Uganda 1° 12′ S 29° 50′ E
Murchison Falls Nat. Park (now Kabalega) W. Uganda 2° 20′ N 31° 40′ E
Nairobi C. Kenya 1° 20′ S 36° 50′ E
Nairobi Nat. Park
Naivasha, Lake C. Kenya 0° 45′ S 36° 20′ E
Nakuru C. Kenya 0° 20′ S 36° 5′ E
Namalusi Is., Port Bell Uganda 0° 19′ N 32° 36′ E
Namaqualand S.W. Africa
Namuli, Mt Mozambique
Napak E. Uganda 2° 8′ N 20′ 34° E
Natal S. Africa
Ngorongoro Crater N. Tanzania 3° 10′ S 35° 35′ E
Ngurdoto Crater 3° 13′ S 36° 52′ E
Nguru Mts E. Tanzania 60° S 37° 30′ E
Nigeria W. Africa
Nimba Mt Guinea and Liberia
Nkata Bay Malawi
Northern Frontier District (N.F.D.) Kenya
Nyanza S.W. Kenya
Nyasa, Lake (Lake Malawi) Central S.E. Africa
Nyika Plateau N. Malawi
Nyiro, Mt Kenya 0° 47′ N 47° E
Nuba Mts Sudan
Okavango Swamp S.W. Africa
Oldonyo Lengai, Mt 2° 46′ S 35° 55′ E
Olduvai Gorge N. Tanzania 3° S 35° 20′ E
Olorgesailie S. Kenya 1° 40′ S 36° 28′ E
Omo S. Ethiopia 5° N 36° E
Oubangui River, marks northern border of Zaire
Pangani River Tanzania Coast 5° 26′ S 38° 58′ E
Pare Mts N. Tanzania
Pemba Is. 4° 50′—5° 30′ S 39° 45′ E
Poroto Mts S.W. Tanzania 9° S 34° E
Queen Elizabeth Nat. Park (now Ruwenzori N.P.) W. Uganda
Rondo Plateau S. Tanzania 10° 10′ S 39° 10′ E
Rovuma River S. Tanzania 10° 45′ S 33° 40′ E 10° S 48° E
Ruaha Park C. Tanzania
Ruaha River System Central and S.E. Tanzania
Ruanda (now Rwanda C. Africa)
Rubeho Mts E. Tanzania
Rudolf, Lake N. Kenya
Rufigi River E. Tanzania 8° 31′ S 37° 22′ E 8° S 39° 25′ E
Rukwa, Lake S.W. Tanzania 7° 35′—8° 32′ S 31° 48′—35° 52′ E
Rungwe, Mt S. Tanzania 9° 8′ S 33° 40′ E
Rusinga Is. Kenya 0° 25′ S 34° 18′ E
Ruwenzori Mts W. Uganda
Sango Bay S. Uganda 0° 55′ S 31° 45′ E
Sankuru River Congo basin
Songwe Caves S.W. Tanzania 8° 50′ S 33° 8′ E

Salisbury, Lake E. Uganda 1° 35′ N 34° 15′ E
Sebei E. Uganda 1° 20′ N 34° 35′ E
Selinda, Mt E. Rhodesia
Semliki Forest Reserve W. Uganda 0° 4′ N 30° E
Semliki River W. Uganda and E. Congo 1° N 30° 20′ E
Senegal W. Africa
Serengeti Nat. Park N. Tanzania
Serengeti Plains N. Tanzania 2° 25′—3° 5′ S 34° 40′—35° 20′ E
Sesse Is. N. Lake Victoria
Shimba Hills 4° 20′ S 39° 35′ E
Shimoni S. Kenya Coast 4° 45′ S 39° 25′ E
Shinyanga C. Tanzania 3° 33′ S 33° 25′ E
Sierra Leone W. Africa
Singo county C. Uganda
Sipi E. Uganda 1° 25′ N 34° 25′ E
Sokoke Forest 3° 15′ S 39° 55′ E
Somalia N.E. Africa
Songea S. Tanzania 10° 42′ S 35° 38′ E
Sotik W. Kenya 0° 40′ S 35° 38′ E
Southern Highlands S.W. Tanzania
Stieglers Gorge Rufigi River 7° 45′ S 37° 50′ E
Suakin Red Sea Coast, Sudan
Suam River, Mt Elgon into Turkwell Gorge Uganda
Suk W. Kenya
Suswa C. Kenya 1° 15′ S 36° 24′ E
Swaziland S. Africa
Tabora C. Tanzania 5° 2′ S 32° 48′ E
Talya River Western slopes of Ruwenzori
Tana River E. Kenya 0°—2° 50′ S 38°—40° 30′ E
Tanga Tanzania Coast 5° 4′ S 39° 6′ E
Tanganyika, Lake E. Africa
Tarangire G.R. N. Tanzania
Taveta S.E. Kenya 3° 20′ S 37° 40′ E
Teso E.C. Uganda
Tiwi Kenya Coast 4° 10′ S 39° 35′ E
Toro W. Uganda
Transvaal S. Africa
Tsavo Nat. Park E. Kenya 3° S 38° 30′ E
Turkana N.W. Kenya
Turkwell River flowing into S. Lake Rudolf
Uelle N.E. Congo (Zaire)
Ufipa S.W. Tanzania 7°—8° S 31° 30′ E
Ugalla River N.W. Tanzania
Ukerewe Is. Lake Victoria 2° S 33° E
Uluguru Mts E. Tanzania 6° 51′ S 37° 44′ E
Upper Guinea W. Africa
Urguess, Mt or Garguess or Warges N. Kenya 0° 58′ N 37° 28′ E
Usambara Mts N.E. Tanzania 5° 6′ S 38° 38′ E
Usangu or Buhoro Flats S.W. Tanzania 8° 30′ S 34° 5′ E

Uvinza W. Tanzania 5° 7′ S 30° 22′ E
Uzungwa Mts C. Tanzania 7° 45′—8° 35′ S 45°—36° 12′ E
Victoria, Lake E. Africa
Virunga Volcanoes W. Uganda and E. Congo 1° 30′ S 29° 35′ E
Voi E. Kenya 3° 28′ S 38° 35′ E
Wami River E. Tanzania 6° 30′ S 37° E—6° S 39° E
Wembere Depression C. Tanzania 3° 45′—5° 10′ S 33° 40′—34° 45′ E
Witu Forest Kenya Coast 2° 25′ S 40° 25′ E
Zaire (Formerly Congo Kinshasha)
Zambesi River S. Africa
Zambia C. Africa
Zanzibar Is. 5° 43′—6° 28′ S 39° 11′—39° 41′ E
Zika Forest Entebbe, Uganda 0° 10′ N 32° 30′ E
Zululand S. Africa

Bibliography

Carnivora

Abbot, S. and Fuller, T. (1971). A fresh look at the cheetah's private life. *Smithsonian* **2** (3), 34–42.

Adamson, G. (1963). Observations on lions in the southern portion of Serengeti National Park mid-June to mid-November 1962. Manuscript in the Tanzania National Parks files.

Adamson, G. (1964). Observations on lions in Serengeti National Park Tanzania. *E. Afr. Wildl. J.* **2**, 160–1.

Adamson, G. (1968). "Bwana Game". Collins, London.

Adamson, J. (1960). "Born Free". Collins, London.

Adamson, J. (1961). "Living Free". Collins, London.

Adamson, J. (1966). Pippa kehrte in die Freiheit zuruck. *Das Tier* **6** (12), 4–7.

Adamson, J. (1969). "The Spotted Sphinx". Collins, London.

Adamson, J. (1972). "Pippa's Challenge". Collins, London.

Aeschliman, A. (1965). Notes on the mammals of the Ivory Coast II. *Afr. Wild life* **19** (1), 37–55.

African adventure (1969). *In* "Window on to Wilderness", (Cullen, A. ed.). East African Publishing House, Nairobi.

Alexander, A. J. and Ewer, R. F. (1959). Observations on the biology and behaviour of the smaller African polecat. *Afr. Wildlife* **13**, 313–20.

Ali, S. (1927). The Moghul emperors of India as naturalists and sportsmen. *J. Bombay Nat. Hist. Soc.* **31** (4), 833–61.

Allen, G. M. (1939). A checklist of African mammals. *Bull. Mus. Comp. Zool. Harvard* **83**, 1–763.

Allen, J. A. (1924). Carnivora collected by the American Museum Congo expedition. *Bull. Amer. Mus. Nat. Hist.* **47**, 73–281.

Andersson, C. J. (1856). "Lake Ngami". Hurst and Blackett, London.

Ansell, W. F. H. (1960a). Contributions to the mammalogy of northern Rhodesia. *Occ. Papers Nat. Mus. S. Rhodesia Nat. Sci.* **3**, 351–98.

Ansell, W. F. H. (1960b). "Mammals of Northern Rhodesia". 31 Government Printer, Lusaka.

Ansell, W. F. H. (1960c). The African striped weasel, *Poecilogale albinucha*, (Gray). *Proc. Zool. Soc. London* **134**, 59–64.

Ansell, W. F. H. (1964). Addenda and corrigenda to "Mammals of Northern Rhodesia" No. 1. *Puku Occ. Papers* **2**, 14–52.

Ansell, W. F. H. (1965). Addenda and corrigenda to "Mammals of Northern Rhodesia" No. 2. *Puku Occ. Papers* **3**, 1–14.

Ansell, W. F. H. (1966). *Atilax paludinosus* in the eastern province. *Puku Occ. Papers* **4**.

Ansell, W. F. H. (1967). An aberrant leopard from Rhodesia. *Arnoldia* **3** (Feb.), 3.

Ansell, W. F. H. (1970). Kitty our slender mongoose. *Black Lechwe* **8**, (July), 3.

Aronson, L. R. and Cooper, M. L. (1966). Seasonal changes in mating behaviour in cats after desensitization of glans penis. *Science N. Y.* **152**, 3719.

Asdell, S. (1964). "Patterns of Mammalian reproduction". Cornell University Press, Ithaca.

Astley Maberly, C. T. (1954). Notes on the only known specimen of the extinct Cape lion. *Afr. Wildlife* **8**, (June), 2.

Astley Maberly, C. T. (1955). The African civet. *Afr. Wildlife* **9**, 55–8.

Astley Maberly, C. T. (1959). "Animals of Rhodesia". Howard Timmings, Cape Town.

Astley Maberly, C. T. (1963). "The Game Animals of Southern Africa." Nelson, Cape Town.

Astley Maberly, C. T. (1968). The rusty-spotted genet. *Natal Wildlife* **9** (2), 22–3.

Azzaroli, L. and Simonetta, A. M. (1966). Carnivori della Somalia ex-italiana. *Monitore Zool. It.* (suppl.) , 102–95.

Babault, G. (1949). Notes éthologiques sur quelques mammifères africains. *Mammalia* **13**, 57–8.

Baker, J. (1960). A trypanosome of *T. congolense* group in African lion and leopard. *Trans. Trop. Med. Hyg.* **54**, 2.

Baker, J. (1968). Trypanosomes of wild mammals in the neighbourhood of the Serengeti National Park. *In* "Diseases in Free-Living Wild Animals" (McDiarmid, A. ed.), Symp. Zool. Soc. London 24, pp. 147–58.

Balcells, R. E. (1956). Datos para el estudio de la geneta. *Publ. Inst. Biol. Barcelona* **23**, 83–122.

Barone, R. (1967). La myologie du lion, *Panthera leo. Mammalia* **31**, 459–514.

Basilio, A. (1962). La vida animal en la Guinea espanola. *Inst. Estud. Afr. Madrid.*

Bates, G. L. (1905). Notes on the mammals of the southern Cameroons and the Benito. *Proc. Zool. Soc. London*, 65–85.

Bauman, F. (1923). Uber *Felis aurata* Temm. Eine eigenartige westafrikanische Katzenart. *Mitt. naturf. Ges. Bern* **8**, 113–18.

Beaton, K. de P. (1949). "A Warden's diary". Nairobi.

Beaufort, F. de (1965). Repartition et taxonomie de la poiane (Viverridae). *Mammalia* **29** (2), 275–80; *and* Taxonomie et repartition de *Pseudogenetta villiersi* Dekeyser 1949. *Mammalia* **29** (2), 281–2.

Beaumont, G. de (1964). Remarques sur la classification des félidés. *Eclog. Geol. Helv.* **57** (2), 837–45.

Beaumont, G. de (1967). Observations sur les Herpestinae (Viverridae Carnivora) de l'Oligocene Superieur avec quelques remarques sur les Hyaenidae du Néogene. *Arch. Sci. Geneve* **20**, 79–107.

Beaumont, R. A. (1969). Some strange observations on the lion. *Redwing*, 8–10.

Beddard, F. E. (1909). Mammalia. *In* "The Cambridge Natural History". Macmillan and Co., London.

Bellier, L., Van Bree P. and Vissault, J. (1972). Quelques données nouvelles concernant le chat doré d'Afrique, *Profelis aurata*, en Côte d'Ivoire. *Biologia gabonica* **8**, 2.

Bentley, T. W. (1971). Predation by *C. mesomelas* on baboon. *Lammergeyer*, **13**.

Bere, R. M. (1956). The African wild dog. *Oryx* **3**, 180.

Bere, R. M. (1962). "The Wild Mammals of Uganda". Longmans, London.

Bernau, U. (1969). Versuche über das Farbsvermögen der Erdmännchen, *Suricata suricatta*. *Z. Säugetierk.* **34**, 223–6.
Bernirschke, K. (1969). Cytogenetics in the zoo. *New Scientist* 16 Jan.
Berrie, P. M. (1973). Ecology and status of the Canada lynx in interior Alaska. *In* "Ecology and Conservation of the World's Cats. (Eaton, R. L. ed.)
Bertram, B. C. R. (1973). Lion population regulation. *E. Afr. Wildl. J.* **11**, 215–25.
Bertram, B. C. R. (1974). Radio-tracking leopards in the Serengeti. *Wildlife News* **9** (2), 7–10.
Bertram, B. C. R. (1975). The social system of lions. *Scient. Amer.* **232**, 54–65.
Bigalke, R. C. (1954). Lions in the Kruger National Park. *Afr. Wildlife* **8**, 1.
Bigalke, R. C. (1961). The size of the litter of the wild dog, *Lycaon pictus*, *Flora and Fauna* **1961**, 9–15.
Bigalke, R. C. and Rowe-Rowe, D. (1969). An analysis of the results of hunting black-backed jackals over a five-year period in Natal. *Lammergeyer* **10**, 70–80.
Blonk, H. L. (1965). Über die afrikanische Goldkatze, *Profelis aurata*. *Säugetierk. Mitt.* **13**, 132–3.
Blower, J. (1962). Wildlife of Uganda 4. Aardwolf. *Wildlife and Sport* **3**, 1. Entebbe, Uganda.
Bone, W. J. (1968). Pansteatitis in a lion, *Felis leo*. *J. Amer. Vet. Med. Ass.* **153**, 791–2.
Booth, A. H. (1959). On the mammalian fauna of the Accra plain. *J. West. Afr. Sci. Ass.* **5**, 26–36.
Booth, A. H. (1960). "Small Mammals of West Africa". Longmans, London.
Boswell, K. (1947). Behaviour of hyaena and panther at a kill. *J. Bombay Nat. Hist.* **47** (2), 366–7.
Bothma, J. du P. (1959). Notes on the stomach contents of certain Carnivora (Mammalia) from the Kalahari Gemsbok Park. *Koedoe* **9**, 37–9.
Bothma, J. du P. (1965). Random observations on the food habits of certain Carnivora (Mammalia) in southern Africa. *Fauna and Flora* **16**, 16–22.
Bothma, J. du P. (1971a). Food of *Canis mesomelas* in South Africa. *Zool. Afr.* **6** (2), 195–203.
Bothma, J. du P. (1971b). Notes on movement by black-backed jackal and the aardwolf in the western Transvaal. *Zool. Afr.* **6** (2), 205–7.
Bouillault, J. and Filloux, J. C. (1955). Une espèce rare en France la genette. *Nature Paris* **3240**, 145–7.
Bourlière, F. (1955). "The Natural History of Mammals". G. Harrap, London.
Bourlière, F. (1962). La structure sociale des meutes de *Lycaon*. *Mammalia* **26**, 167–70.
Bourlière, F. (1963). Specific feeding habits of African carnivores. *Afr. Wildlife* **17**, 21–7.
Bourlière, F. (1964). Densities and biomass of some ungulate populations in eastern Congo and Rwanda. *Zool. Afr.* **1**.
Brehm, A. (1915). "Tierleben" Vol. 12. Leipzig and Wien.
Brehm, A. (1927). "Das Leben der Tiere: Die Säugetiere. Berlin.
Brentjes, B. (1962). Mensch und Katze im Alten Orient. *Wiss. Zschr. Univ. Halle Wittenberg.*

Brentjes, B. (1966). Einige Bemerkungen zur Darstellung der Hyänen, Erdwolfe und Hyänenhunde im Kulturen des Alten Orientes. *Z. Säugetierk.* **31**, 308–14.
Brocklehurst, H. C. (1931). "Game Animals of the Sudan". Gurney and Jackson, London.
Brocklesby, D. W. and Vidler, B. O. (1965). Some parasites of East African wild animals. *E. Afr. Wildl. J.* **3**, 120–2.
Brockman, R. E. D. (1910). "Mammals of Somaliland". Hurst and Blackett, London.
Brooks, A. C. (1962). Uganda's small mammals II. The small cats. *Wildlife and Sport* **3** (2), 8–11.
Brown, L. (1965). "Africa. A Natural History". Hamilton, London.
Bruckner, R., Sutter, E., Hurter, G. and Schenkel, R. (1961). Über die Netzhaut von Feliden und Caniden. *Biol. Zbl.* **80**, 37–66.
Bryant, J. (1959). Value of otters. *Field, London* **196**, 833.
Bryden, H. A. (1905). "Big Game Shooting". H. G. Hutchinson, London.
Buckland-Wright, J. C. (1969). Craniological observations on *Hyaena* and *Crocuta*. *J. Zool. London* **59**, 17–29.
Budgett, H. M. (1933). "Hunting by Scent". Eyre and Spottiswoode, London.
Burton, R. W. (1952). The "dew claws" of the cheetah. *J. Bombay Nat. Hist. Soc.* **49** (3).
Butler, A. M. (1914). Notes on the lion in the Sudan. *In* "Book of the Lion". (Pease ed.), London.
Butler, P. (1946). The evolution of carnassial dentitions in the Mammalia. *Proc. Zool. Soc. London* **116**, 198–220.
Cade, C. E. (1967). Notes on breeding the Cape hunting dog, *Lycaon pictus*, at Nairobi Zoo. *Int. Zoo. Yearbook* **7**, 122–3.
Cade, C. E. (1968). A note on breeding the caracal lynx, *Felis caracal*, at Nairobi Zoo. *Int. Zoo Yearbook* **8**, 45.
Calmette, A. (1907). "Les Venins". Paris.
Cansdale, G. S. (1946). "Animals of West Africa". Longmans, London.
Cantle *In* Simpson, C. D. (1964). *Arnoldia* **1**, 1–8.
Carpenter, G. C. (1970). Observations on rusty-spotted genet. *Lammergeyer* **11**.
Carvalho de C. (1968). Comparative growth rates of hand-reared big cats. *Int. Zoo Yearbook* **8**, 56–9.
Champion, F. W. (1936). Ratels and corpses. *J. Bombay Nat. Hist. Soc.* **39**, 159–61.
Cloete, R. C. *In* Sclater, W. L. (1900). "The Mammals of South Africa", Vols I and II. H. Porter, London.
Coaton, W. G. H. (1948). *Trinervitermes* species – The snouted harvester termites. *Bull. Dep. Agric. For. Un. S. Afr. Ent. ser.* 23, **271**, 1–19.
Coetzee, C. G. (1967). Carnivora. *In* "Preliminary Identification Manual for African Mammals", 7. (excluding the family Felidae). Smithsonian Institution, Washington.
Coetzee, C. G. (1969). The distribution of mammals in the Namib desert and adjoining inland escarpment. *Sci. Pap. Namib Desert Research St.* **4** (40), 23–36.
Colbert, E. H. (1939). Origin of the dog. *Nat. Hist.* **43**, 90–101.

Cole, L. C. (1960). Competitive exclusion. *Science* **132**, 348.
Cooke, H. S. B. (1963). Pleistocene mammal fauna of Africa with particular reference to southern Africa. *In* "African Ecology and Human Evolution" (Howell, F. C. and Bourlière, F. eds). Viking Fund Publications in Anthropology, No. 36, New York.
Cooper, A. L. (1927). Notes on *Acinonyx rex* (Cooper's cheetah). *S. Afr. J. Sci.* **24**, 343–5.
Cooper, J. (1942). An exploratory study on African lions. *Comp. Psychol. Monograph* **17** (7), 1–48.
Cope, E. D. (1888). The mechanical origin of the sectorial teeth of the Carnivora. *Proc. Amer. Ass. Adv. Sci.* **36**, 254–7.
Copley, H. (1950). "Small Mammals of Kenya". Highway Nature Guides. Highway Press, Nairobi.
Corbett, J. (1956). "The Man-eating Leopard of Rudraprayag". Oxford University Press.
Coryndon, S. C. and Savage, R. J. G. (1973). Origins and affinities of African mammal faunas. *In* "Organisms and Continents through Time". Special papers in Palaeontology, No. 12. *Syst. Ass. Publ.* **9**, 121–35.
Cott, H. (1940). "Adaptive Coloration in Animals". Methuen, London.
Cowie, M. (1961). National Parks of Kenya Annual Report, Nairobi.
Cowie, M. (1966). "The African Lion". Gólden Press, New York.
Crandall, L. S. (1964). "The management of Wild Animals in Captivity". University of Chicago Press.
Criddle, S. (1947). A nest of the least weasel. *Can. Fld Nat.* **61**, 69.
Critchley, R. A. (1965). Wild dog family. *Black Lechwe* (Sept.).
Crusafont Pairo, M. and Truyols, S. J. (1957). El "grades" de los carnivoros en el cuaternario a partir de la cladogenesis y anagenesis de este order de mamiferos. *Conf. int. Ass. Quatern. Res.* **35**.
Cullen, J. M. (1969). "Window on to Wilderness". Nairobi East African Publishing House.
Cumming, R. G. (1850). "Five Years of a Hunter's life". Murray, London.
Dalton, M. (1961). Chiro a mongoose pet. *Wildlife* December 1960-March 1961.
Darling, F. (1969). An ecological reconnaissance of the Mara Plains in Kenya colony. *Wildl. Monogr.* **5**.
Darlington, P. (1957). "The Geographical Distribution of Mammals". John Wiley and Sons Inc., New York.
Davis, D. D. (1949). The female external genitalia of the spotted hyaena. *Fieldiana Zool.* **31** (33), 277–83.
Davis, R. K. (1967). The criteria for rational land use. Paper to East Africa Wildlife Land Use Symposium, Nairobi, July.
Deane, N. N. (1960). Hyaena predation. *Lammergeyer* **1** (1), 36.
Deane, N. N. (1962). The spotted hyaena, *Crocuta crocuta crocuta*. *Lammergeyer* **2** (2), 26–43.
Debbie, J. G. (1970). Report No. TA2834 to Govt Kenya on wildlife disease research. FAO, U.N., Rome.
Deevey, E. (1969). Coaxing history to conduct experiments. *Bioscience* **19**, 40–3.

Dekeyser, P. L. (1945). À propos des chats de l'Afrique noire française. *Mammalia* **9**, 51–60.
Dekeyser, P. L. (1951). La tête osseuse chez les chakals d'Afrique orientale française. *Bull. Inst. Fr. Afr. Noire* **13**, 2.
Dekeyser, P. L. (1955). "Les Mammifères de l'Afrique Noire Française". Inst. Fr. Afr. Noire, Dakar.
Dekker, D. (1968). Breeding the Cape hunting dog at Amsterdam Zoo. *Int. Zoo Yearbook* **8**, 27–30.
Denis, A. (1964). "Cats of the World". Constable and Co. London.
Denyer, L. C. (1962). Pack hunting by jackals. *Lammergeyer* **1** (1).
Didier, R. (1946). Étude systématique de l'os pénien des mammifères: Carnivores Canidés. *Mammalia* **10**.
Didier, R. (1947, 1948). Étude systématique de l'os pénien des mammifères: Mustelidés. *Mammalia* **11** and **12**.
Didier, R. (1949). Étude systématique de l'os pénien des mammifères: Félidés *Mammalia* **13**.
Dinnick, J. A. and Sachs, R. (1969). Zystizerkose der Kreuzbeinwirbel bei Antilopen und *Taenia olngojinei* sp. nov. der Tüpfelhyäne. *Z. Parasitenk.* **31**, 326–39.
Dobroruka, L. J. (1965). Zur Verbreitung des "Sansibar Leoparden", *Panthera p. adersi*. *Z. Säugertierk.* **30**, 144–6.
Dobroruka, L. J. (1966). Ein Beitrag zur Kenntniss südafrikanischer Leoparden, *Panthera pardus* (Linn.). *Säugetierk. Mitt.* **14** (4), 317–24.
Dominis, J. and Edey, M. (1968). "The Cats of Africa". Time Life Books Inc., New York.
Donovan, C. A. (1967). Some clinical observations on sexual attraction and deterrence in dogs and cattle. *Vet. Med.* **62**, 1047–51.
Donovan, C. A. (1969). Canine anal glands and chemical signals. *J. Amer. Vet. Med. Ass.* **155**, 1995–6.
Dorst, J. and Dandelot, P. (1970). "A Field Guide to the Larger Mammals of Africa". Collins, London.
Dücker, G. (1957). Farb- und Helligkeitssehen und Instinkte bei Viverriden und Feliden. *Zool. Beitr.* **3**, 25–99.
Dücker, G. (1960). Beobachtungen über das Paarungsverhalten des Ichneumons, *Herpestes ichneumon* L. *Z. Säugetierk.* **25**, 47–51.
Dücker, G. (1962). Brutpflegverhaltung und Ontogenese des Verhaltens bei Surikaten, *Suricata suricatta* Schreb., Viverridae. *Behaviour* **14**, 305–40.
Dücker, G. (1965). Das Verhalten der Viverriden. *Handb. Zool. Berl.* **8** (38), 1–48.
Dulton, T. P. (1962). Water mongoose feeding. *Lammergeyer* **2** (1).
Duplaix Hall, N. *In* Ewer, R. F. (1973). "The Carnivores". Weidenfeld and Nicolson, London.
Durrell, G. (1954). "The Bafut Beagles". Rupert Hart-Davis, London.
Durrell, G. (1960). "A Zoo in my Luggage". Rupert Hart-Davis, London.
Eaton, R. L. (1969a). The cheetah. *Africana* **3** (10), 19–23.
Eaton, R. L. (1969b). Cooperative hunting by cheetahs and jackals and a theory of domestication of the dog. *Mammalia*, 33.
Eaton, R. L. (1969c). The social life of the cheetah. *Animals* **12**, 172–5.

Eaton, R. L. (1969d). Hunting relationships of cheetahs with non-prey species. *Mammalia* **33**, 543–4.
Eaton, R. L. (1970a). Group interactions, spacing and territoriality in cheetah. *Z. Tierpsychol.* **27** (4), 481–91.
Eaton, R. L. (1970b). The predatory sequence, with emphasis on killing behaviour and its ontogeny in the cheetah, *Acinonyx jubatus* Schreb. *Z. Tierpsychol.* **27** (4), 492–504.
Eaton, R. L. (1970c). Hunting behaviour of the cheetah. *J. Wildl. Mgmt* **34** (1), 56–67.
Eaton, R. L. (1970d). Notes on the reproductive biology of the cheetah. *Int. Zoo Yearbook* **10**, 86–89.
Eaton, R. L. (1972). An experimental study of predatory and feeding behaviour in the cheetah, *Acinonyx jubatus*. *Z. Tierpsychol.* **31**, 270–80.
Eaton, R. L. (1973). "The World's Cats". Vol. I "Ecology and Conservation". World Wildlife Safari, Winston, Ore.
Eaton, R. L. (1974). "The Cheetah. The Biology, Ecology and Behaviour of an Endangered Species". Van Nostrand Reinhold Co., New York.
Eibl-Eibesfeldt, I. (1950). Über die Jugendentwicklung des Verhaltens eines männlichen Dachses, *Meles meles* L., unter besonderer Berücksichtigung des Spieles. *Z. Tierpsychol.* **7**, 327–55.
Eibl-Eibesfeldt, I. (1955). Zur Biologie des Iltis. *Verh. Dtsch. Zool. Ges. Erlangen* **1955**, 304–14.
Eisenberg, J. F. and Kleiman, D. G. (1972). Olfactory communication in mammals. *Am. Rev. Ecol. Syst.* **3**, 1–32.
Eisenberg, J. F. and Lockhart, M. (1972). An ecological reconnaissance of Wilpattu National Park, Ceylon. *Smithsonian Contributions to Zoology* **101**.
Eisner, T. (1968). Mongoose and millipede. *Science* **160**, 1367.
Eisner, T. and Davis, J. A. (1967). Mongoose throwing and smashing millipedes. *Science* **155**, 577–9.
Ellerman, J. R., Morrison-Scott, T. C. S. and Hayman, R. W. (1953). Southern African Mammals 1758–1951: A Reclassification. British Museum (Nat. Hist.) London.
Elliot, D. G. (1883). "A Monograph of the Felidae". Private ed. London.
Eloff, F. C. (1964). On the predatory habits of lions and hyaenas. *Koedoe* **7**, 105–12.
Eloff, F. C. (1973). Lion predation in the Kalahari Gemsbok National Park. Paper given at the S. Africa Wildlife Mgmt. Ass. Symposium June 1973. Pretoria.
Erlinge, S. (1967a). Home range of the otter, *Lutra lutra* L. in southern Sweden. *Oikos* **18**, 186–209.
Erlinge, S. (1967b). Food habits of the fish-otter, *Lutra lutra* in South Swedish habitats. *Viltrevy* **4**, 372–443.
Erlinge, S. (1968a). Territoriality of the otter, *Lutra lutra* L. *Oikos* **19**, 81–98.
Erlinge, S. (1968b). Food studies on captive otters, *Lutra lutra* L. *Oikos* **19**, 259–70.
Erlinge, S. (1969a). Food habits of the otter, *Lutra lutra* L. and the mink, *Mustela vison* Schreb. in a trout water in southern Sweden. *Oikos* **20**, 1–7.

Errington, P. L. (1967). "Of Predation and Life". Iowa State University Press.

Estes, R. D. (1967). Predators and scavengers. *Nat. Hist.* **76** (2), 20–9; **76** (3), 38–47.

Estes, R. D. and Goddard, J. (1967). Prey selection and hunting behaviour of the African wild dog. *J. Wildl. Mgmt* **31** (1), 52–70.

Ewer, R. F. (1948). The fossil carnivores of the Transvaal caves. Canidae. *Proc. Zool. Soc. London* **126**, 97–120.

Ewer, R. F. (1954). Some adaptive features in the dentition of hyaenas. *Ann. Mag. Nat. Hist.* **12** (7), 188–194.

Ewer, R. F. (1955a). The fossil carnivores of the Transvaal caves. The Lycyaenas of Sterkfontein and Swartkrans, together with some general considerations of the Transvaal fossil hyaenids. *Proc. Zool. Soc. London* **124**, 839–57.

Ewer, R. F. (1955b). The fossil carnivores of the Transvaal caves: Machairodontinae. *Proc. Zool. Soc. London* **125**, 587–615.

Ewer, R. F. (1956). The fossil carnivores of the Transvaal caves: Canidae. *Proc. Zool. Soc. London* **126**, 97–119.

Ewer, R. F. (1963). The behaviour of the meerkat *Suricata. Z. Tierpsychol.* **20**, 570–607.

Ewer, R. F. (1965). Carnivora. *In* "Olduvai Gorge 1951–61" (Leakey, L. S. B. *et al.*), Cambridge University Press.

Ewer, R. F. (1967). The fossil hyaenids of Africa, a reappraisal. *In* "Background to Evolution in Africa", (Bishop, W. and Clark, J. D. eds). University of Chicago Press.

Ewer, R. F. (1968). "Ethology of Mammals". Logos Press, London.

Ewer, R. F. (1973). "The Carnivores". Weidenfeld and Nicolson, London.

Ewer, R. F. and Cooke, H. B. S. (1964). The Pleistocene mammals of southern Africa. (Davis, D. H. S., ed.), Monographiae Biologicae XIV The Hague, pp. 35–48.

Eyre, M. (1963a). "Otter in our Parlour". Tafelberg–Uitgewers, Capetown. (1963b). A tame otter. *Afr. Wildlife* **17**, 4953.

Fairall, N. (1968). The reproductive seasons of some mammals in the Kruger National Park. *Zoologica Africana* **3**, 189–210.

Faust, R. (1969). Lebensdauer und Geburten eines serval Weibchens, *Leptailurus serval. Zool. Garten Lpz.* **37**, 150.

Fey, V. (1964). The diet of leopards. *Afr. Wildlife* **18**, 105–9.

Fiedler, W. (1957). Beobachtungen zum Markierungsverhalten einiger Säugetiere. *Z. Säugetierk.* **22**, 57–76.

Fischer, C. E. C. (1921). The habits of the grey mongoose. *J. Bombay Nat. Hist. Soc.* **28**, 274.

Fleetwood, J. D. L. (1958). The ratel. *J. E. Afr. Nat. Hist. Soc.* **23**, 11–12.

Florio, P. and Spinelli, L. (1967). Successful breeding of a cheetah in a private zoo. *Int. Zoo Yearbook* **7**, 150–2.

Florio, P. and Spinelli L. (1968). Second successful breeding of cheetahs in a private zoo. *Int. Zoo Yearbook* **8**, 76–8.

Flower, W. H. (1869). On the anatomy of the proteles, *Proteles cristatus* Sparrman. *Proc. Zool. Soc. London* **1869**, 474–96.

Flower, W. H. (1872). Note on the anatomy of the two-spotted paradoxure, *Nandinia binotata*. *Proc. Zool. Soc. London* **1872**, 683–4.

Fooks, H. A. (1952). The leopard's spots. *Field* **200**, 550.

Foran, W. R. (1952). Melanism and altitude. *Field* **199**, 542 and 950.

Fosbrooke, H. (1963). The *Stomoxys* plague in Ngorongoro 1962. *E. Afr. Wildl. J.* **1**, 124–6.

Fosbrooke, H. (1967). Hyaena incident. *Black Lechwe* **6** (3), 29–31.

Foster, J. and Coe, M. (1968). The biomass of game animals in Nairobi National Park 1960–66. *J. Zool. London* **155** (4), 413–25.

Foster, J. and Kearney, D. (1967). Nairobi National Park game census 1966. *E. Afr. Wildl. J.* **5**, 112–20.

Foster, J. and McLaughlin, R. (1968). Nairobi National Park game census 1967. *E. Afr. Wildl. J.* **6**, 152–4.

Fox, M. W. (1969). The anatomy of aggression and its ritualization in canids. *Behaviour* **35**, 242–58.

Fox, M. W. (1970). A comparative study of the development of facial expression in canids; wolf, coyote and foxes. *Behaviour* **36** (1–2), 49–73.

Fox, M. W. (1971a). "Behaviour of Wolves and Dogs and Related Canids". Jonathan Cape, London.

Fox, M. W. (1971b). Ontogeny of social display in *Hyaena hyaena* anal protrusion. *J. Mammal.* (May), 467.

Fox, M. W. (1974). "The Wild Canids: Their Systematic Behavioural Ecology Evolution. Van Nostrand Reinhold, New York.

Fremer, H. von Ketelhodt (1965). Aardwolf food and behaviour. *Afr. Wildlife* **19**.

Fremer, H. von Ketelhodt (1966). *Proteles*. *Z. Säugetierk.* **31**, 300–6.

Friedman, H. (1955). The honey-guides. *Bull. U. S. Nat. Mus.* **208**, 1–292.

Frobenius, L. E. (1954). "Kulturgeschichte Afrikas". Zurich.

Fuente, de La R. (1970). "World of Wildlife Series". Orbis, London.

Fuente, de La R. (1972). "World of Wildlife" I, "Africa. Hunters and Hunted of the Savannah". Orbis, London.

Gaspard, M. (1964). La région de l'angle mandibulaire chez les Canidae. *Mammalia* **28**, 249–329.

Gee, E. P. (1961). Some notes on the golden cat, *Felis aurata* (Temm.) *J. Bombay Nat. Hist. Soc.* **58**, 508–11.

Gensch, W. (1962). Successful rearing of the binturong, *Artictis binturong* (Raffl.). *Int. Zoo Yearbook* **4**, 79–80.

Gensch, W. (1966). Nochmals zur Nachzucht des Binturong, *Artictis binturong* (Raffl.) im Zoologischen Garten Dresden. *Zool. Garten Lpz.* **33**, 126–8.

Gesner, C. (1563). "Tierbuch". Zurich.

Gidayatov, Y. K. (1969). Ecology of *Canis aureus* in Azerbaijan. *Izvestai Akad. Nauk. Azerbaidzhanskoi USSR ser. biol.* **1969** (1), 57–64.

Goethe, F. (1964). Das Verhalten der Musteliden. *Handb. Zool. Berlin* **37**, 1–80.

Golani, I. (1966). Observations on the behaviour of the jackal, *Canis aureus*, in captivity. *Israel Zool.* **15**, 28.

Golani, I. and Mendelsshon, H. (1971). Sequences of precopulatory behaviour of the jackal, *Canis aureus*. *Behaviour* **38** (1–2), 169–92.

Gowda, C. D. K. (1967). A note on the birth of a caracal lynx, *Felis caracal*, at Mysore Zoo. *Int. Zoo Yearbook* **7**, 133.

Grafton, R. (1965). Food of the black-backed jackal; a preliminary report. *Zool. Afr.* **1** (1), 41–53.

Graham, A. (1966). East African Wildlife Society cheetah survey: extracts from the report by Wildlife Services. *E. Afr. Wildl. J.* **4**, 50–5.

Gray, A. P. (1971). "Mammalian Hybrids". Commonwealth Africultural Bureau, Slough, pp. 1–262.

Gregory, W. K. and Hellman, M. (1939). On the evolution and major classification of the civets (Viverridae) and allied fossil and recent Carnivora: a phylogenetic study of the skull and dentition. *Proc. Amer. Philos. Soc.* **81**, 309–92.

Grzimek, B. (1972). "Animal Life Encyclopedia" (Grzimek, ed.). Van Nostrand Reinhold, New York.

Grzimek, B. and Grzimek, M. (1960). A study of the game of the Serengeti plains. *Z. Säugetierk* **25**, 1–61.

Guggisberg, C. A. W. (1961). "Simba, the Life of the Lion". Howard Timmings, Capetown.

Guggisberg, C. A. W. (1966–68). Beobachtungen am ostafrikanischen Leoparden, *Panthera pardus*. *Jb. Naturh. Mus. Bern*, 122–36.

Guilday, J. E. (1962). Supernumerary molars of *Otocyon*. *J. Mammal.* **43**, 455–62.

Hafez, E. S. E. (1962). "The Behaviour of Domestic Animals". Williams and Wilkins Co., Baltimore.

Haffner, *et al.* (1969). *In* Debbie, J. G. (1970).

Hallet, J. P. and Ellis, F. E. (1960). Python and aardwolf. *Wildlife, Nairobi* **2** (3), 28–9.

Haltenorth, T. (1957). "Die Wildkatze". Neue Brehm Bucherei.

Haltenorth, T. (1958). "Rassehunde-Wildhunde". Winter Heidelberg.

Haltenorth, T. and Trense, W. (1956). "Das Grosswild der Erde und seine Trophäen". Bayerischer Landwirtschaftsverlag, Bonn.

Hamilton, P. (1974). The Tsavo leopard project. *Wildlife News* **9**(2), 2–6.

Hamilton, P. (1976). The movements of leopards in Tsavo National Park, Kenya as determined by radio-tracking. MSc. Thesis, University of Nairobi.

Hanström, B. (1949). Cheetahs provide an unusual experience. *Afr. Wildl. J.* **3** (3), 203–9.

Harris, C. J. (1968). "Otters". Weidenfeld and Nicolson, London.

Harris, L. (1971). "Cats of the Wild, Great and Small". Ward Ritchie Press, Los Angeles.

Harrison, D. L. *In* Swynnerton, C. F. M. (1936).

Hartwig, E. K. (1955). Control of snouted harvester termites. *Fmg. S. Afr.* **30**.

Hayman, R. W. (1949). One cat or two? *Zoo Life, Lond.* **4**, 7–8.

Hediger, H. (1949). Säugetier-Territorien und ihre Markierung. *Bjd. Dierk.* **28**, 172–84.

Hediger, H. (1950). "Wild Animals in Captivity". Butterworth, London.

Hediger, H. (1951). "Observations sur la Psychologie Animale dans les Parcs Nationaux du Congo Belge". No. 1, pp. 1–194. Hediger and Verschuren, Bruxelles.

Heimburger, N. (1959). Das Markierungsverhalten einiger Caniden. *Z. Tierpsychol.* **16**, 104–13.

Heisch, R. B., Graniger, W. E., Harvey, A. E. C. and Lister, G. (1962). Feral aspects of rickettsial infections in Kenya. *Trans. R. Soc. Trop. Med. Hyg.* **56**, 272–82.

Hendey, Q. B. (1974). The late Cenozoic Carnivora of the South-western Cape Province. *Ann S. Afr. Mus.* **63**, 1–369.

Hendrichs, H. (1972). Beobachtungen und Untersuchungen zur Ökologie und Ethologie insbesondere zur sozialen Organization ostafrikanischer Säugetiere. *Z. Tierpsychol.* **30**.

Herdman, R. (1972). Captive cheetah reproduction. *Zoonoz* **45**, 10.

Herschkovitz, P. (1969). The evolution of mammals on southern continents VI. The recent mammals of the neotropical region: a zoogeographic and ecological review. *Q. Rev. Biol.* **44**, 1–70.

Hescheler, K. and Kuhn, E. (1949). Die Tierwelt der prähistorischen Siedlungen der Schweiz. *Tschumi, Urgeschichte der Schweiz.* **I**.

Hewson, R. (1969). Couch building by otters, *Lutra lutra*. *J. Zool.* **159**, 524–7.

Heye, A. (1927). Neun Afrikanische Plagen. *Kosmos* **24** *Jahrgang Heft* 6.

Hildebrant, M. (1952). An analysis of body proportions in the Canidae. *Amer. J. Anat.* **90**, 217–256.

Hildebrant, M. (1954). Comparative morphology of the body skeleton in recent Canidae. *Univ. Calif. Publ. Zool.* **52**, 399–470.

Hildebrant, M. (1959). Motions of the running cheetah and horse. *J. Mammal.* **40**, 481–95.

Hildebrant, M. (1960). How animals run. *Scient. Amer.* **202**, 148–157.

Hildebrant, M. (1961). Further studies on locomotion of the cheetah. *J. Mammal.* **42**, 84–91.

Hildebrant, M. (1968). Symmetrical gaits of dogs in relation to body build. *J. Morph.* **124**, 353–60.

Hill, C. A. (1965). A is for aardwolf. *Zoonooz* **38**, 11.

Hillaby, J. (1967a). Apemen, artefacts and hyaenas. *New Scientist* 27 April.

Hillaby, J. (1967b). The superbeast of prey. *New Scientist* 14 December.

Hinton, H. E. and Dunn, A. M. S. (1967). "Mongooses. Their Natural History and Behaviour". University of California Press.

Hinton, M. A. C. (1921a). *Paraonyx*. A new genus of clawless otter. *Ann. Mag. Nat. Hist.* (9) **7**, 194–200.

Hinton, M. A. C. (1921b). Some new African mammals. *Ann. Mag. Nat. Hist.* (9) **7**, 368.

Hirst, S. M. (1969). Predation as a regulating factor of wild ungulate populations in a Transvaal low veld nature reserve. *Zoologica Africana* **4**, 199–230.

Hoesch, W. (1964). Beobachtungen an einem zahmen Hönigdachs, *Mellivora capensis*. *Zool. Garten Lpz.* **28** (4), 182–8.

Hollister, N. (1917). Some effects of environment and habit on captive lions. *Proc. U.S. Nat. Mus.* **53**.

Holz, H. (1964). Zur innerartlichen Variabilität und phylogenetischen Stellung des Afrikanischen Hyänenhundes *Lycaon pictus*. *Zool. Anz.* **174**, 362–95.

Hoogstraal, H. (1964). A brief review of the contemporary land mammals of Egypt (including Sinai). *J. Egypt Publ. Hlth. Ass.* **39**.

Hoogstraal, H., Wassif, K., Helmy, I. and Kaiser, M. (1966–67). The cheetah, *Acinonyx jubatus*, in Egypt. *Bull. Soc. Zool. Egypt* **21**, 63–8.

Hooijer, D. A. (1952). The cave hyaena, *Crocuta crocuta spelaea* (Goldfuss) new to the Pleistocene fauna of the Netherlands. *Geol. Mijnb.* **14**, 385–8.

Hooijer, D. A. (1963). Miocene mammalia of the Congo. *Amst. Mus. Roy. Afr. Cent. Śer.* 8 *Sci. Geol.* **46**, 1–77.

Hopwood, A. T. (1947a). Contribution to the study of some African mammals VI. Notes on the interior of the skull in lion, leopard and cheetah. *J. Linn. Soc. Zoology* **41**, 369–76.

Hopwood, A. T. (1947b). Adaptations in the bones of the forelimb of the lion, leopard and cheetah. *J. Linn. Soc. Zoology* **41**, 259–71.

Hopwood, A. T. and Hollyfield, J. P. (1952). An annotated bibliography of the fossil mammals of Africa, No. 8, pp. 1–194. British Museum (Nat. Hist.) London.

Hornocker, M. G. (1969). Winter territoriality in mountain lion. *J. Wildl. Mgmt* **33**, 457–64.

Hornocker, M. G. (1970). An analysis of mountain lion predation. *Wildl. Monogr.* **21**.

Hoyle, A. C. (1955). *Webbia* **11**, 493.

Huf, K. (1962). Über das Verhalten des Binturong, *Artictis binturong*. Diss. in Druck.

Hunt, R. M. (1974). The auditory bullae in Carnivora. An anatomical basis for reappraisal of carnivore evolution. *J. Morph.* **5**, 143, 1, 21–76.

Hunter, J. (1960). The rapacious wild dog. *Wildlife* **2** (1), 42.

Hurrell, E. (1963). Watch for the otter. *Country Life*, London.

Inglis, C. M. (1951). Some wild cats. *J. Bengal Nat. Hist. Soc.* **25**, 1–6.

Ionides, C. J. P. (1935). Provincial Game Warden's Annual Report. Tanganyika Game Dept.

Ionides, C. J. P. (1948). Mammal notes. Some interesting animals of Kenya 4. *Nature E. Afr.* **7**, 10–12.

Ionides, C. J. P. (1965). "A Hunter's Story". W. H. Allen, London.

Jackson, F. J. J. (1938). "The Birds of the Kenya Colony and the Uganda Protectorate". Gurner and Jackson, London and Edinburgh.

Jacobsen, E. J. *In* Ewer, R. F. (1973). "The Carnivores". Weidenfeld and Nicolson, London.

James, A. (1950). Rhodesian leopards and record weight. *Field* **195**, 805.

Jeannin, A. (1936). Les mammifères sauvages du Cameroun. *Encyclop. Biol.* **16**.

Jearey, B. (1936). "Pride of Lions". Longmans, London.

Jewell, P. (1966). The concept of home range in mammals. *In* "Play, Exploration and Territory in Mammals" (Jewell, P. and Loizos, C. eds). Symp. Zool. Soc. London 18, pp. 85–109. Academic Press, London and New York.

Jobaert, A. J. (1960). Le leopard. *Zooleo* **56**, 223–30.

John, E. P., Chesler, P., Bartlett, F. and Victor, I. (1968). Observation learning in cats. *Science* **159** (3822), 1489–91.

Johnson, C. E. (1964). *In* Debbie, J. G. (1970). Report No. T.A. 2834 to Govt. Kenya on wildlife disease research. FAO U.N. Rome.
Johnson, M. (1929). "Lion". G. P. Putman's Sons, New York.
Johnson, M. (1935). "Over African Jungles". Harrap, London.
Johnson, R. R. (1973). Scent marking in mammals. *Anim. Behav.* **21** (3), 521–35.
Jordan, P., Shelton, P. and Allen, D. (1967). Numbers, turnover and social structure of the Isle Royale wolf population. *Amer. Zool.* **7**, 232–52.
Jugle, J. (1949). Cheetahs as pets. *Field* **1949**, 440.
Jux, U. and Rosenbauer, K. A. (1960). Untersuchungen zur postfetalen Entwicklung des Schadels von *Hyaena spelaea. Z. Morph. Anthrop.* **51**, 45–53.
Kaufmann, J. (1962). Ecology and social behaviour of the coati, *Nasua narica*, on Barro Colorado island Panama. *Univ. Calif. Publ. Zool.* **60** (3), 95–222.
Kearton, C. (1929). "In the Land of the Lion". Arrowsmith, London.
Keimer, L. (1942). Quelques representations rarissimes des mustelidés. Études d'Egyptologie IV, Cairo.
K.G.R. Kenya Government Reports (1922–1975).
K.N.P.R. Kenya National Parks Reports 1960–1966.
Kernerknechts, S. (1940). Die Hohlenhyäne 3. Das Gliedmassenskelet. *Abh. Zool. Bot. Ges.* **17**, 192–260.
Kernerknechts, S. and Ehrenberg, K. (1940). Die Fuchs-oder Teufels lucken bei Eggenburg Niederdonau. *Abh. Zool. Bot. Ges.* **17** (2), 131–91.
Kirby, P. R. (1940). The Diary of Dr A. Smith Director of the Expedition for Exploring Central Africa 1834–36. The van Riebeeck Society, Capetown.
Kleiman, D. G. (1966a). Comparative social behaviour of Canidae. *Amer. Zool.* **6**, 355.
Kleiman, D. G. (1966b). Scent Marking in the Canidae. *In* "Play, Exploration and Territory in Mammals" (Jewell, P. and Loizos, C. eds). Symp. Zool. Soc., London, 18, pp. 167–77. Academic Press, London and New York.
Kleiman, D. G. (1967). Some aspects of social behaviour in Canidae. *Amer. Zool.* **7**, 365–72.
Kleiman, D. G. and Eisenberg, J. F. (1973). Comparisons of canid and felid social systems from an evolutionary perspective. *Anim. Behav.* **21**, 637–59.
Kling, A., Kovak, J. K. and Tucker, T. J. (1969). The behaviour of cats. *In* Hafez "The Behaviour of Domestic Animals". Baillière Tindall and Cassel.
Koenigswald, G. H. von (1965). Das Leichenfeld als Biotop. *Zool. Jb. Syst.* **92**, 73–82.
Kock, L. de (1965). Rinja the honey badger. *Animals* **7** (12).
Kortlandt, A. (1967). Experimentation with chimpanzees in the wild. "Progress in Primatology". Fisher.
Kostin, V. P. (1963). On the distribution and ecology of *Mellivora* in southern Ust-Uit. *Zool. Zh.* **42**, 307–8 (in Russian).
Kovach, J. and Kling, A. (1967). Mechanisms of neonate sucking behaviour in the kitten. *Anim. Behav.* **15** (1), 91–101.

Krumbiegel, I. (1952). Der Löwe. *Neue Brehm Büch.* **30**.
Kruuk, H. (1965a). A kill in the Serengeti. *Animals* **7**, 189–91.
Kruuk, H. (1965b). Masai art. *Animals* **6** (18), 494–9.
Kruuk, H. (1966a). A new view of the hyaena. *New Scientist* **30**, 849–51.
Kruuk, H. (1966b). Clan system and feeding habits of spotted hyaenas, *Crocuta crocuta* (Erxl.) *Nature* **209**, 1257–8.
Kruuk, H. (1970). Interactions between populations of spotted hyaenas, *Crocuta crocuta* (Erxl.) and their prey species. *In* "Animal Populations in Relation to their Food Resources" (Watson, A. ed.) Blackwell, Oxford.
Kruuk, H. (1972a). Surplus killing by carnivores. *J. Zool.* **166** (2).
Kruuk, H. (1972b). "The Spotted Hyaena". University of Chicago Press, Chicago and London.
Kruuk, H. (1975). "Hyaena". Oxford University Press, Oxford and London.
Kruuk, H. and Sands, W. A. (1972). The aardwolf (*Proteles cristatus* Sparrman) 1783 as predator of termites. *E. Afr. Wildl. J.* **10** (3), 211–27.
Kruuk, H. and Turner, M. (1967). Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti area, East Africa. *Mammalia* **31**, 1–27.
Kühme, W. (1964a). Die Ernährungsgemeinschaft des Hyänenhundes *Lycaon pictus lupinus* Thomas 1902. *Naturwissenschaften* **20**, 495.
Kühme, W. (1964b). Über die soziale Bindung innerhalb eines Hyänenhund-Rudels. *Naturwissenschaften* **51**.
Kühme, W. (1965a). Freilandstudien zur Soziologie des Hyänenhundes *Lycaon pictus lupinus* Thomas 1902. *Z. Tierpsychol.* **22** (5), 495–541.
Kühme, W. (1965b). Communal food distribution and division of labour in African hunting dogs. *Nature* **205**, 443–4.
Kühme, W. (1966). Beobachtungen zur Soziologie des Löwen in der Serengeti steppe Ostafrikas. *Z. Säugetierk.* **31** (3), 205–13.
Kurten, B. (1957). *Percrocuta kretzoi* (Mammalia Carnivora) a group of Neogene hyaenas. *Acta Zool. Cracov.* (2) **16**, 375–404.
Kurten, B. (1958). The bears and hyaenas of the interglacials. *Quarternaria* **4**, 69–81.
Kurten, B. (1968). "Pleistocene Mammals of Europe". Weidenfeld and Nicolson, London.
Lack, D. (1954). "The Natural Regulation of Animal Numbers". Clarendon Press, Oxford.
Lammergeyer (1962). Banded mongoose feeding. Note by McDonald, L. J. *Lammergeyer* **2** (1), 68.
Lamprey, H. F. (1962). A study of the ecology of the mammal population of a game reserve in the acacia savanna of Tanganyika with particular reference to animal numbers and biomass. PhD Thesis. Univ. Mus. Oxford.
Lamprey, H. F. (1963). Ecological separation of the large mammal species in the Tarangire Game Reserve. *E. Afr. Wildl. J.* **1**, 63–9.
Lamprey, H. F. (1964). Examination of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai steppe in Tanganyika. *E. Afr. Wildl. J.* **2**, 1–46.
Lang, E. M. (1963). Wie jagt der Hyänenhund (*Lycaon pictus*). *Z. Säugetierk.* **28**, 314–15.

Lanham, T. *In* Shortridge, G. (1934). "The Mammals of South West Africa". Heinemann, London.
Lawick, van H. (1970). "Innocent Killers". Collins, London.
Lawick, van H. (1974). "Solo". Collins, London.
Lawrence, B. and Bosser, W. H. (1967). Multiple character analysis of Canis lupus, latrans and familiaris. *Amer. Zool.* **7**, 223–32.
Layard, H. (1887). "Early Adventures in Persia, Susiana and Babylon". London.
Leakey, L. S. B. (1947). Notes on mammals. The golden cat. *Nature E. Afr.* **1** (8).
Leakey, L. S. B. (1969). "Animals of East Africa". National Geographic Society, Washington.
Leuw, A. (1957). Die Wildkatze. *Merkbl. Niederwildauss dtsc. Jagdschutzverb.* **16**.
Leyhausen, P. (1950). Beobachtungen an Löwen-Tiger-Bastarden mit einigen Bemerkungen zur Systematik des Grosskatzen. *Z. Tierpsychol.* **7** (1), 48–83.
Layhausen, P. (1956). Verhaltensstudien an Katzen. *Z. Tierpsychol. Beiheft* **2**, 1–120.
Leyhausen, P. (1965a). The Communal Organisation of Solitary Mammals. *In* "Social Organization of Animal Communities" (Ellis, P. ed.). Symp. Zool. Soc. London 14, pp. 249–63. Distributed by Academic Press, London and New York.
Leyhausen, P. (1965b). Über die Funktion der relativen Stimmunghierarchie. *Z. Tierpsychol.* **22**, 412–94.
Leyhausen, P. and Wolff, R. (1959). Das Revier einer Hauskatze. *Sonderdruck aus Z. Tierpsychol.* **16** (6), 666–70.
Leyn, G. (1962). "Contribution à la connaissance des Lycaons au Parc national de la Kagera". Inst. Parcs nat. Congo et du Rwanda, Bruxelles.
Liers, E. E. (1951). Notes on the river otter, *Lutra canadensis*. *J. Mammal.* **32**, 1–9.
Lindemann, W. (1955). Über die Jugendentwicklung beim Luchs (*Lynx 1. lynx* Kerr) und bei der Wildkatze (*Felis s. sylvestris* Schreber) *Behaviour* **8**, 1–45.
Linley, T. A. (1965). Aardwolf at East London Zoo. *Int. Zoo Yearbook* **5**.
Lloyd-Jones, W. T. (1951). Habits of the mongoose. *J. Bombay Nat. Hist. Soc.* **50**, 397–8.
Lockie, J. D. (1966). Territory in small carnivores. *In* "Play, Exploration and Territory in Mammals" (Jewell, P. and Loizos, C. eds). Symp. Zool. Soc. London 18, pp. 143–65. Academic Press, London and New York.
Lombard, G. L. (1958). The water mongoose (*Atilax*). *Fauna and Flora Transvaal.* **9**, 24–7.
Lord, W. (1953). The Cape hunting dog. *Field* **201**, 1953.
Lousada, A. (1956). Rearing serval cats. *Country Life, London* **120**, 330–1.
Loveridge, A. (1921–22). Notes on East African mammals (other than the horned ungulates) collected or kept in captivity 1915–19. 2 parts. *J. E. Afr. Nat. Hist. Soc.* **16** (38); **17** (39).
Loveridge, A. (1923). Notes on East African mammals collected 1920–23. *Proc. Zool. Soc. London.*

Loveridge, A. (1933). Field notes in Allen and Loveridge: Reports on the scientific results of an expedition to the southwestern highlands of Tanganyika territory, II: Mammals. *Bull. Mus. Comp. Zool. Harvard* **75**.

Loveridge, A. (1936). Field notes. *In* Allen and Lawrence. Scientific results of an expedition to the rain forest regions of eastern Africa, III: Mammals. *Bull. Mus. Comp. Zool. Harvard* **79**, 31.

Loveridge, A. (1951). "Tomorrow's a Holiday". Robert Hale, London.

Lyddeker, R. (1907). Notes on two African mammals. *Proc. Zool. Soc. Lond.* **1907**, 782–5.

Lyddeker, R. (1912). On the milk dentition of the ratel. *Proc. Zool. Soc. Lond.* **1912**, 221–4.

Lyddeker, R. (1926). "The Game Animals of Africa". Rowland Ward, London.

Lynch, J. J. (1971). Of dogs and men. The physiology of companionship. *Scientific American*.

Maberly (*see* Astley Maberly).

MacInnes, D. G. (1952). Melanism and mongooses (letter). *Field* **199**, 62.

MacIntosh, E. (1953). The Cape hunting dog (letter). *Field* **201**, 640.

MacIntyre, G. T. (1966). The Miacidae (Mammalia Carnivora). *Bull. Amer. Mus. Nat. Hist.* **131**, 115–210.

Maglio, V. (1972). Vertebrate fauna and chronology of hominid bearing sediments east of Lake Rudolph, Kenya. *Nature* **239**, 379–85.

Makacha, S. and Schaller, G. B. (1969). Observations on lions in the Lake Manyara National Park, Tanzania. *E. Afr. Wildl. J.* **7**, 99–103.

Malbrant, R. and Maclatchy, A. (1949). Faune de l'Équateur africain français II. Mammifères. *Encyclop. Biol.* **36**, 1–323.

Mallison, J. J. C. (1967). Notes on the breeding of the African civet. *Rep. Jersey Wildl. Pres. Trust* **4**, 22–4.

Mallison, J. J. C. (1973). The reproduction of the African civet in Jersey Zoo. *Int. Zoo Yearbook* **13**.

Matthew, W. D. (1910). The phylogeny of the Felidae. *Bull. Amer. Mus. Nat. Hist.* **28**, 289–316.

Matthew, W. D. (1930). The phylogeny of dogs. *J. Mammal.* **11**, 117–38.

Matthews, L. H. (1939a). The bionomics of the spotted hyaena, *Crocuta crocuta* Erxl. *Proc. Zool. Soc. London* 43–56.

Matthews, L. H. (1939b). Reproduction in the spotted hyaena, *Crocuta crocuta* Erxl. *Philos. Trans. B.* **230**, 1–78.

Matthews, L. H. (1939–41). *Phil. Trans. Roy. Soc. London* **109**, A.

Matthews, L. H. (1959). "The Mammals" 2 vol. Weidenfeld and Nicolson.

Maxwell, G. (1960). "Ring of Bright Water". Longmans, London.

Maxwell, G. (1961). The lives and times of Mij and Edal. *Nat. Hist. N.Y.* **70** (3), 50–61.

Mazak, V. (1968). Note sur les caractères craniens de la sous-famille des Pantherinae. *Mammalia* **32** (4), 670–6.

Mckenna, M. C. (1975). Towards a phylogenetic classification of the Mammalia. *In* "Phylogeny of the Primates". (Luckett, J. and Szalay, F. S. eds),

McLaughlin, R. T. (1970). Aspects of the biology of the cheetahs (*Acinonyx*

jubatus Schreber) in Nairobi National Park. M.Sc. Thesis, University of Nairobi.

Mcmaster, A. N. *In* Shortridge, G. (1934). "The Mammals of South West Africa". Heinemann, London.

Mcnab, B. (1963). Bio-energetics and determination of home range sizes. *Amer. Nat.* **97**, 133–40.

Meinertzhagen, R. (1957). "Kenya Diary 1902–1906". Edinburgh and London.

Mensch, van P. J. A. and van Bree, P. J. H. (1969). On the African golden cat, *Profelis aurata* Temm. *Biologia Gabonica* **5**, 235–69.

Mertens, R. (1954). Zum Problem der Färbung von *Lycaon pictus* Temm. *Z. Säugetierk* B **2** (Kleine Mitteilungen). 32–3.

Merwe, Van der N. J. (1954). The jackal. *Fauna and Flora Pretoria* **4**.

Merwe, Van der N. J. (1959). Die Wildehond, *Lycaon pictus*. *Koedoe* **2** S, 87.

Michael, R. R. (1958). Sexual behaviour and the vaginal cycle in the cat. *Nature* **181**, 567–8.

Michael, R. R. (1961). Observations on the sexual behaviour of the domestic cat, *Felis catus*, under laboratory conditions. *Behaviour* **18**.

Michaelis, B. (1972). Die Schleichkatzen (Viverriden) Afrikas. *Sonderdruck Säugtierk Mitt.* **1**, 1–110.

Mitchell, B. L., Shenton, J. B. and Uys, J. C. (1965). Predation on large mammals in the Kafue National Park Zambia. *Zoologica Africana* **1**.

Mohr, E. (1961a). Der Zahnschluss im Gebiss der Wildraubtiere und der Haustiere. *Z. Säugetierk.* **22**, 151–82.

Mohr, E. (1961b). Undershot and overshot lower jaws in Carnivora. *Z. Säugetierk.* **26**, 50–6.

Moreau, R. E. (1966). "The Bird Faunas of Africa and its Islands". Academic Press, London and New York.

Morrison-Scott, T. C. S. (1952). The mummified cats of ancient Egypt. *Proc. Zool. Soc. Lond.* **121**, 861–7.

Mortimer, M. A. E. (1963). Notes on the biology and behaviour of the spotted-necked otter, *Lutra maculicollis*. *Puku* **1**, 192–206.

Moss, C. (1976). "Portraits in the Wild". Collins, London.

Muckenhirn, N. A. and Eisenberg, F. F. (1973). "Home Ranges and Predation of the Ceylon leopard. Proc. 1st Int. Symp. Ecol. Behav. and Conservation of the world's cats (Eaton, R. L., ed.), pp. 142–75. World Wildlife Safari, Oregon.

Murray, M. (1967). The pathology of some diseases found in wild animals in East Africa. *E. Afr. Wildl. J.* **5**, 37–45.

Myers, N. (1974a). An evaluation of the status of the cheetah. *Afr. Wildlife* **9** (2).

Myers, N. (1974b). The leopard hangs tough. *Inter. Wildlife* **4** (6), 4–12.

Myers, N. (1975). The cheetah, *Acinonyx jubatus* in Africa. *IUCN Monograph* **4**.

Myers, N. (1976). The leopard *Panthera pardus* in Africa. *IUCN Monograph* **5**.

Nasimovich, A. A. (1949). The biology of the weasel in the Kola peninsula in connection with its competitive relations with the ermine. *Zool. Zh.* **28**, 177–82.

Naundorff, E. (1936). Über *Chrossarchus obscurus* als Hausgenossen. Carnivoren Studien 2. *Kleintier Pelztier. Lpz.* **12**, 97–102.

Neal, E. (1970a). The banded mongoose, a little known carnivore. *Animals* **13**, 29–31.

Neale, E. (1970b). The banded mongoose, *Mungos mungo* Gmelin. *E. Afr. Wildl. J.* **8**, 29–31.

Neseni, R. and Heidler, G. (1966). Ernährungsphysiologische Untersuchungen an Zootieren. *Zool. Garten Lpz.* **33** (1–3), 110–18.

Neubert, O. (1957). "The Valley of the Kings". London.

Novikov, G. A. (1956). Carnivorous mammals of the fauna of the USSR (English translation). *Israel Programme for Scientific Translations*, Jerusalem 1962.

Ognev, S. I. (1931). Mammals of eastern Europe and northern Asia Vol. II Carnivora. *Israel Programme for Scientific Translations*, Jerusalem 1962.

Orts, S. G. (1970). Le *Xenogale* de J. A. Allen (Carnivora, Viverridae) au sujet d'une capture effectuée au Kivu. *Rev. Zool. Bot. Afr.* **82**, 174–86.

Osborn, D. J. (1968). Hyaena hunt. *Bull. Field. Mus. Nat. Hist.* **39** (3).

Palen, G. and Goddard, G. (1966). Catnip and oestrous behaviour in the cat. *Anim. Behav.* **14** (2–3), 372–7.

Patterson, J. H. (1907). "The Man-eaters of Tsvao". Macmillan, London.

Pearsall, W. (1957). Report on an ecological survey of the Serengeti National Park, Tanganyika. *Fauna Preserv. Soc. London.*

Pearson, O. (1964). Carnivore-mouse predation: an example of its intensity and bioenergetics. *J. Mammal.* **45** (2), 177–88.

Pearson, P. P. and Baldwin, P. H. (1953). Reproduction and age structure of a mongoose population in Hawaii. *J. Mammal.* **34**, 436–47.

Pease, A. (1914). "The Book of the Lion". John Murray, London.

Pennycuick, C. G. and Rudnai, J. A. (1970). A method of identifying individual lions, *Panthera leo*, with an analysis of the reliability of identification. *J. Zool. London* **160**, 497–508.

Percival, A. B. (1924). "A Game Ranger's Notebook". J. Nisbet and Co., London.

Percival, A. B. (1928). "A Game Ranger on Safari". J. Nisbet and Co., London.

Petter, F. (1957). La reproduction du fennec. *Mammalia* **21**, 307–9.

Petter, F. (1959). Reproduction en captivité du zorille du Sahara, *Poecilictis lybica*, *Mammalia* **23**, 378–80.

Petter, G. (1964). Origine du genre *Otocyon* (Canidae) africain de la sous-famille des Otocyoninae. *Mammalia* **28** (2), 330–44.

Petter, G. (1969). Interprétation évolutive des caractères de la denture des viverridés africains. *Mammalia* **33**, 607–25.

Petter, G. (1973). Carnivores pleistocènes du Ravin d'Olduvai (Tanzania). *In* "Fossil Vertebrates of Africa". Vol. 3. (Leakey, L. S. B., Savage, R. J. G. and Coryndon, S. C., eds), pp. 43–100. Academic Press, London and New York.

Petter, G. and Howell, F. C. (1976). Origine et radiation du genre *Acinonyx* (Carnivora Felidae) dans les formations pleistocènes d'Afrique, d'Europe et d'Asie. *C. R. Acad. Sci Paris* **282**.

Petzsch, H. (1955). Zum Problem der Färbung von *Lycaon pictus* Temminck 1820. *Kleine Mitteilungen 3. Säugetierk.* 82–3.
Petzsch, H. (1963). Zum Problem ungewonlicher Haarerwechsel bei gefangenen Säugetieren. *Zool. Garten. Lpz.* **27**, 135.
Petzsch, H. (1971). "Die Katzen" 2 vols. Urania, Berlin.
Pfeffer, P. (1972). Observations sur le comportement social et predateur du *Lycaon pictus* en Republique Centreafricaine. *Mammalia* **36** (1).
Pienaar, U. de V. (1961). A second outbreak of anthrax amongst game animals in the Kruger National Park. 5th June to October 1960. *Koedoe* **4**, 4–14.
Pienaar, U. de V. (1963). The large mammals of the Kruger National Park, their distribution and present day status. *Koedoe* **6**, 1–37.
Pienaar, U. de V. (1964). The small mammals of the Kruger National Park, a systematic list and zoogeography. *Koedoe* **7**, 1–26.
Pienaar, U. de V. (1969). Predatory-prey relationships amongst the larger mammals of the Kruger National Park. *Koedoe* **12**, 108–87.
Pienaar, U. de V., Le Riche, E. and Le Roux, C. S. (1969). The use of drugs in the management and control of large carnivorous mammals. *Koedoe* **12**, 188–93.
Pilleri, G. (1967). Retinalfalten im Auge von Wasseraugentiere. *Experientia* **23**, 54–5.
Pimental, D. (1955). Biology of the Indian mongoose in Puerto Rico. *J. Mammal.* **36**, 62–8.
Pimlott, D. (1967). Wolf predation and ungulate populations. *Amer. Zool.* **7**, 267–78.
Pimlott, D., Shannon, J. and Kolenosky, G. (1969). The ecology of the timber wolf in Algonquin Provincial Park. Dept. Lands and For. Ontario.
Pitman, C. R. S. (1931). Annual Report of the Game Department. Government Printer, Entebbe, Uganda.
Pitman, C. R. S. (1935). Annual Report of the Game Department. Government Printer, Entebbe, Uganda.
Pitman, C. R. S. (1936). Annual Report of the Game Department. Government Printer, Entebbe, Uganda.
Pitman, C. R. S. (1942). "A Game Warden Takes Stock". J. Nisbet and Co., London.
Pitman, C. R. S. (1951). Annual Report of the Game Department. Government Printer, Entebbe, Uganda.
Pitman, C. R. S. (1954). African genets and mongooses. *Zoo Life, London* **9**, 9–12.
Piveteau, J. (1961). Traité de Paléontologie **6** (1). Masson and Cie, Paris.
Plessis, du S. S. (1972). Ecology of the blesbok on the Vn Riebeck Nature Reserve. D.Sc. Thesis. Pretoria.
Pocock, R. I. (1970a). Notes upon some African species of the genus *Felis* based upon specimens recently exhibited in the Society's gardens. *Proc. Zool. Soc. London.*
Pocock, R. I. (1907b). Report upon a small collection of mammalia brought from Liberia by Mr Leighton. *Proc. Zool. Soc. London.*
Pocock, R. I. (1908). Warning coloration in the musteline Carnivora. *Proc. Zool. Soc. London.*

Pocock, R. I. (1911). Some probable and possible instances of warning characteristics amongst insectivorous and carnivorous mammals. *Ann. Mag. Nat. Hist.* **8**, 750–7.

Pocock, R. I. (1914). On the feet and other external features of the Canidae and Ursidae. *Proc. Zool. Soc. London.*

Pocock, R. I. (1915a). On the feet and glands and other external characters of the Viverrinae, with the description of a new genus. *Proc. Zool. Soc. London* 131–49.

Pocock, R. I. (1915b). On the feet and glands and other external characters of the paradoxurine genera, *Paradoxurus, Artictis, Arctogalidia* and *Nandinia*. *Proc. Zool. Soc. London*, 387–412.

Pocock, R. I. (1916a). On some of the external structural characters of the stripes hyaena, *Hyaena hyaena*, and related genera and species. *Ann. Mag. Nat. Hist.* **17**, 330–43.

Pocock, R. I. (1916b). On some cranial and external characters of the hunting leopard or cheetah, *Acinonyx jubatus*. *Ann. Mag. Nat. Hist.* **18**, 419–29.

Pocock, R. I. (1916c). On the external characters of the mongooses (Mungotidae). *Proc. Zool. Soc. London*, 349–74.

Pocock, R. I. (1917). On the external characters of the Felidae. *Ann. Mag. Nat. Hist.* **19**, 113–36.

Pocock, R. I. (1920). On the external characters of the ratel (*Mellivora*) and the wolverine (*Gulo*). *Proc. Zool. Soc. London.*

Pocock, R. I. (1921). On the external characters and classification of the Mustelidae. *Proc. Zool. Soc. London*, 803–37.

Pocock, R. I. (1927a). The external characters of the South African striped weasel, *Poecilogale albinucha*. *Proc. Zool. Soc. London*, 125–33.

Pocock, R. I. (1927b). Description of a new species of cheetah (*Acinonyx*) *Proc. Zool. Soc. London*, 245–52.

Pocock, R. I. (1932). The leopards of Africa. *Proc. Zool. Soc. London*, 543.

Pocock, R. I. (1935). The races of the striped and brown hyaenas. *Proc. Zool. Soc. London*, 799.

Pocock, R. I. (1944a). The races of the north African wild cat, *Felis lybica*, *Proc. Zool. Soc. London* **114** (1 and 2), 65–73.

Pocock, R. I. (1944b). The wild cat, *Felis lybica*, of northern Baguella Angola. *Ann. Mag. Nat. Hist.* **11**, 130–3.

Pocock, R. I. (1944c). The South African races of wild cat, *Felis lybica*, *Proc. Zool. Soc. London* **114** (3), 297–301.

Pocock, R. I. (1951). Catalogue of the genus *Felis*. *Brit. Mus. Nat. Hist. London.*

Pohle, H. (1920). Die Unterfamilie der Lutrinae. *Arch. Naturgeschich.* **1919** A9, **85**, 1–247.

Poole, T. B. (1973). The aggressive behaviour of individual male polecats (*Mustela putorius*, *M. furo* and hybrids) towards familiar and unfamiliar opponents. *J. Zool. London* **170**.

Pournelle, G. H. (1965). Observations on birth and early development of the spotted hyaena. *J. Mammal.* **46**, 503.

Pournelle, G. H. (1967). The hyaena and the aardwolf, a family dispute *Zoonooz* **40**, 11, 8–12.

Powell, J. E. (1913). Notes on the habits of the small Indian mongoose, *Mungos auropunctatus*. *J. Bombay Nat. Hist. Soc.* **22**.
Powell, A. N. W. (1964). The phiao (*Canis aureus*). *J. Bengal Nat. Hist. Soc.* **33**, 136–42.
Prickett, R. J. (1974). "The African Ark". David and Charles, Newton Abbot.
Pringle, J. A. (1968). Our mongooses. *Natal Wildlife* **9** (2), 12–14.
Prins, I. (1954). Aperçu sur l'histoire de l'industrie européenne de la civette. *Coll. Acad. Intern. Hist. Sci.* **8**, 493–7.
Preston, F. W. (1950). Mongoose luring guineafowl. *J. Mammal.* **31**, 194.
Procter, J. (1963). A contribution to the natural history of the spotted-necked otter (*Lutra maculicollis* Lichtenstein) in Tanganyika. *E. Afr. Wildl. J.* **1**, 92–102.
Rahm, U. (1966). Les mammifères de la forêt équatoriale de l'est du Congo. *Ann. Mus. Roy. de l'Afr. centrale. Tervuren Sciences Zoologiques* **149**.
Rahm, U. and Christiaensen, A. (1963). Les mammifères de la région occidentale du lac Kivu. *Ann. Mus. Roy. Afrique central. Sciences Zoologiques* **118**.
Rainsford, W. (1909). "The Land of the Lion". Doubleday, New York.
Rasa, O. A. E. (1972). Aspects of social organisation in captive dwarf mongooses. *J. Mammal.* **53** (1), 181–5.
Rasa, O. A. E. and Ewer, R. F. (1973). *In* "The Carnivores". Weidenfeld and Nicolson, London.
Rasa, O. A. E. (1973a). Intra-familial sexual repression in the dwarf mongoose, *Helogale parvula*. *Die Naturwissenschaften* **6**, 303–4.
Rasa, O. A. E. (1973b). Prey capture, feeding techniques and their ontogeny in the African dwarf mongoose, *Helogale*. *Z. Tierpsychol.* **32** (5), 449–88.
Rensch, B. and Dücker, G. (1959). Die Spiele von *Mungo* und *Ichneumon*. *Behaviour* **14**, 185–213.
Reuther, R. and Doherty, J. (1968). Birth seasons of mammals at San Francisco Zoo. *Int. Zoo Yearbook* **8**, 97–101.
Rheingold, H. L. (1963). "Maternal Behaviour in Mammals". John Wiley, New York.
Roberts, A. (1951). "The Mammals of South Africa". Central News Agency, Capetown.
Robinette, W., Gashwiler, J. and Morris, O. (1961). Notes on cougar productivity and life history. *J. Mammal.* **42** (2), 204–17.
Robinson, R. (1969a). The breeding of spotted and black leopards. *J. Bombay Nat. Hist. Soc.* **66**, 423–9.
Robinson, R. (1969b). The white tigers of Rewa. *Carnivore Genet. Newsl.* **8**, 192–3.
Rode, P. (1939). Mensurations et poids des gros mammifères d'après le Col. R. Meinertzhagen. *Mammalia* **3**.
Roeder, G. (1936). Das Ichneumon in der ägyptischen Religion und Kunst. *Zschr. Religion* **4**.
Romer, A. S. (1928). Pleistocene animals of Algeria. Fauna of the Palaeolithic station of Mechta-el-Arbi. *Bull. Logan. Mus.* **1**, 80–163.
Romer, A. S. (1945). "Vertebrate Palaeontology". University of Chicago Press.

Romer, A. S. (1968). "Notes and Comments on Vertebrate Palaeontology". University of Chicago Press.

Rood, J. P. (1974). Banded mongoose male guard young. *Nature, London* **248**, 176.

Rood, J. P. (1975). Population dynamics and food habits of the banded mongoose. *E. Afr. Wildl. J.* **13**, 89–111.

Roosevelt, T. (1910). "African Game Trails". New York.

Roosevelt, T. and Heller, E. (1915). "Life Histories of African Game Animals". London.

Rose, F. (1953). The case for white leopards. *Field* **101**, 635.

Rosenberg, H. (1971). Breeding the bat-eared fox, *Otocyon megalotis*, at Utica Zoo. *Int. Zoo Yearbook* **11**.

Rosenzweig, M. L. (1968). The strategy of body-size in carnivores. *Am. Midland Natur.* **30** 299–315.

Rosevear, D. R. (1974). "The Carnivores of West Africa". Trustees of the British Museum (Nat. Hist.) London.

Roth, W. T. (1964). A re-evaluation of *Panthera pardus adusta*. *Zool. Garten Lpz.* **29**, 283–4.

Rowe-Rowe, D. T. (1969). Some observations on a captive African weasel *Poecilogale albinucha*. *Lammergeyer* **10**, 93–6.

Rowe-Rowe, D. T. (1971). The development and behaviour of a rusty-spotted genet *Genetta rubiginosa* Pulcheran. *Lammergeyer* **13**, 29–44.

Rowe-Rowe, D. T. (1972). The African weasel *Poecilogale albinucha* Gray in southern Africa. *Lammergeyer* **15**.

Rudnai, J. A. (1970). Social behaviour and feeding habits of lion *Panthera leo massaica* Neumann in Nairobi National Park. MSc. thesis University of Nairobi.

Rudnai, J. A. (1973a). Reproductive biology of lions (*Panthera leo massaica*) Neumann in Nairobi National Park. *E. Afr. Wildl. J.* **11**, 241–53.

Rudnai, J. A. (1973b). "The Social Life of the Lion". Medical and Technical Publishing Co., Lancaster, England.

Rudnai, J. A. (1973c). The pattern of lion predation in Nairobi National Park. Mimeographed.

Saba, A. R. K. (1974). The ecology of lions (*Panthera leo massaicus* Neumann) in the Masai Mara Game Reserve, Kenya. MSc. thesis University of Nairobi.

Sachs, R. (1967). Liveweights and body measurements of Serengeti game animals. *E. Afr. Wildl. J.* **5**, 24–36.

Sachs, R. (1969). Untersuchungen zur Artbestimmung und Differenzierung der Muskelfinnen ostafrikanischer Wildtiere. *Z. Tropenmedizin und Parasitologie* **20** (1), 39–50.

Sachs, R., Schaller, G. and Baker, J. (1967). Isolation of trypanosomes of the *T. brucei* group from the lion. *Acta Tropica* **24** (2), 109–12.

Sachs, R., Staak, C. and Groocock, C. (1968). Serological investigation of brucellosis in game animals in Tanzania. *Bull. Epizoot. Dis. Afr.* **16**, 93–100.

Sadlier, R. (1966). Notes on reproduction in the larger Felidae. *Int. Zoo Yearbook* **6**.

Sapozhenkov, Y. F. (1961). On the ecology of *Felis lybica* in eastern Kara-Kuny. *Zool. Zh.* **40**, 1585–6.
Sapozhenkov, Y. F. (1962). The ecology of the caracal in the Karakoum. *Zool. Zh.* **41**, 1111–12.
Sapozhenkov, Y. F., Gorelov, Y. K., Zhernovoi, I. V. and Svyatoi, V. I. (1963). On the distribution and ecology of *Mellivora* in Turcmenia. *Zool. Zh.* **42**, 961–4.
Saunders, J. K. (1963). Food habits of the lynx in Newfoundland. *J. Wildl. Mgmt* **27**, 384–90.
Savage, R. J. C. (1965). Fossil Mammals of Africa 19. Miocene Carnivora of East Africa. *Bull. Brit. Mus. Nat. Hist.* **10**, 242–300.
Savage, R. J. C. "Fossil Carnivora of Africa" (in press).
Scapino, R. P. (1968). Biomechanics of feeding in Carnivora. *Diss. Abstr.* **29** B.
Schaller, G. B. (1960). The role of the scavengers and predators. *Wildlife Nairobi* **2** (2), 27–8.
Schaller, G. B. (1966). Progress report on Serengeti lion study. *E. Afr. Wildlife Soc. Newsletter.*
Schaller, G. B. (1967). "The Deer and the Tiger". University of Chigaco Press.
Schaller, G. B. (1968). Hunting behaviour of the cheetah in the Serengeti National Park, Tanzania. *E. Afr. Wildl. J.* **6**, 95–100.
Schaller, G. B. (1969). Life with the king of beasts. *National Geogr.* **135** (4).
Scaller, G. B. (1970). This gentle and elegant cat. *Nat. Hist.* **79** (6), 31–9.
Schaller, G. B. (1972a). Predators of the Serengeti. *Nat. Hist.* **81** (2), 49; **81** (3), 60–69; **81** (4), 38–43.
Schaller, G. B. (1972b). "The Serengeti Lion: A Study of Predator-Prey Relations". University of Chicago Press.
Schaller, G. B. (1973). "Serengeti: A Kingdom of Predators". Collins, London.
Schaller, G. B. (1974). "Golden Shadows Flying Hooves". Collins, London.
Schaller, G. B. and Lowther, G. (1969). The relevance of carnivore behaviour to the study of early hominids. *S. W. J. Anthrop.* **25** (4), 307–41.
Schenkel, R. (1947). Ausdruckstudien an Wolfen. *Behaviour* **1**, 81–129.
Schenkel, R. (1966a). Zum Problem der Territorialität und des Markierens bei Säugern am Beispiel des schwarzen Nashorns und des Löwens. *Z. Tierpsychol.* **23** (5), 595–626.
Schenkel, R. (1966b). Play, exploration and territoriality in the wild lion. *In* "Play, Exploration and Territory in Mammals" (Jewell, P. and Loizos, C. eds). Symp. Zool. Soc. London **18**, pp. 11–12. Academic Press, London and New York.
Schenkel, R. (1967). Submission: Its features and function in the wolf and dog. *Amer. Zool.* **7**, 319–329.
Schneider, K. M. (1926). Über Hyänenzucht. *Die Peltztierzucht* **2** (8), 1–4.
Schneider, K. M. (1952). Einige Bilder zur Paarung der Fleckenhyäne *Crocuta crocuta* Erxl. *Zool. Garten Lpz.* **19**, 135–49.

Schouteden, H. (1944–46). De Zoogdieren van Belgisch Congo en van Ruanda-Urundi. Tervuren *Ann. Mus. Congobelge Zoologie série* **2** (3), 1–576.

Schouteden, H. (1947). Notes sur quelques Félidès melanisants du Congo. *Rev. Zool. Bot.* **40**, 89–95.

Schouteden, H. (1950). Vue d'ensemble sur la zoologie du Congo Belge. *3 Rep. Ann. de l'IRSAC.*

Schreitmüller, W. (1942–49). Einiges uber zahme Fischottern (*Lutra lutra* L.) *Z. Säugetierk.* **17**.

Schumacher, G. H. (1961). "Funktionelle Morphologie der Kaumuskulatur". Fischer, Jena.

Sclater, W. L. (1900). "The Mammals of South Africa" Vols I, II. H. Porter, London.

Scott, J. P. (1967). The evolution of social behaviour in dogs and wolves. *Amer. Zool.* **7**, 373–81.

Scott, J. P. and Fuller, J. L. (1965). "Genetics and Social Behaviour of the Dog". University of Chicago Press.

Scott, K. (1959). Bathing by spotted hyaenas in Uganda. *J. Mammal.* **40**.

Seitz, A. (1959). Beobachtungen an Handaufgezogenen Goldschakalen (*Canis aureus aligirensis. Z. Tierpsychol.* **16**, 747–71.

Selous, F. (1908). "African Nature Notes and Reminiscences". Macmillan, London.

Sheppard, P. M. (1964). Natural selection and mimicry. *Discovery* **25** (1).

Shoener, T. (1969). Models of optimal size for solitary predators. *Amer. Nat.* **103** (931).

Shortridge, G. (1934). "The Mammals of South West Africa". Heinemann, London.

Sikes, S. K. (1963). The self-confident ratel. *Anim. Kingdom* **66**.

Sikes, S. K. (1964). The ratel or honey badger. *Afr. Wildlife* **18**, 29–37.

Simon, N. (1962). "Between the Sunlight and the Thunder". Collins, London.

Simon, N. (1966). Red Data Book, Vol. I Mammalia. IUCN Morges, Switzerland.

Simons, J. W. (1966). The presence of leopard and a study of the food debris in the leopard lairs of the Mt Suswa caves, Kenya. *Bull. Cave Explor. Group E. Afr.* **1**.

Simpson, C. D. (1964). Notes on the banded mongoose *Mungos mungo. Arnoldia* **1**, 1–8.

Simpson, C. D. (1966). The banded mongoose. *Anim. Kingdom* **69**.

Simpson, G. G. (1945). The principle of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* **85**, 1–350.

Sjead, D. M. (1973). Incidence of calling in the black-backed jackal. *J. S.A. Wildlife Mgmt Ass.* **3** (1), 28–9.

Smiles, P. (1961). "A Game Ranger's Notebook". Blackie, London and Glasgow.

Smith, A. *In* Kirby, P. R. (1940). "The Diary of Dr A. Smith etc". The van Riebeeck Society, Capetown.

Smith, L. J. (1967). The aardwolf. *Zoonooz* 8.

Smith, R. (1963). Leopard chased by a hyaena. *Field and Tide* **4**.

Smithers, R. H. N. (1966a). A southern bat-eared fox. *Anim. Kingdom*. **69**.
Smithers, R. H. N. (1966b). "The Mammals of Rhodesia, Zambia and Malawi". Collins, London.
Smithers, R. H. N. (1966c). "Matusana" a bat-eared fox. *Anim. Kingdom* **69**.
Smithers, R. H. N. (1967). Museum contributions to Mammalogy. *S. Afr. Mus. Ass. Bull.* **8** (14).
Smithers, R. H. N. (1968a). A check list and atlas of the mammals of Botswana Trustees of the National Museum, Rhodesia.
Smithers, R. H. N. (1968b). Carnivora, Felidae. *In* "Preliminary Identification manual for African Mammals". Smithsonian Institution, Washington.
Smithers, R. H. N. (1968c). Cat of the Pharaohs. *Anim. Kingdom* **61**, 16–23.
Smithers, R. H. N. (1971). "The Mammals of Botswana". Mem. nat. Mus. Rhodes. No. 4.
Sokolov, I. I. Origin and systematic position of the Mustelidae family and the major trends of its evolution. *Byull. Mosk. Obshch. Ispyt Prir* **76** (6), 5–16.
Southern, N. H. (1964). (ed.) "The Handbook of British Mammals". Blackwells, Oxford.
Spannhof, I. (1969). The histophysiology and function of the anal sac of the red fox. *Forma et Functio* **1**.
Sparrman, A. (1784). "Reise nach dem Vorgebirge den Guten Hoffnung (etc.)" 1784.
Speke, J. H. (1863). "The Journal of the Discovery of the Source of the Nile". Blackwood, Edinburgh and London.
Spinelli, N. (1970). Handrearing of an aardwolf. *Int. Zoo Yearbook* **10**.
Spinelli, P. and Spinelli, L. (1968). Second successful breeding of cheetahs in a private zoo. *Int. Zoo Yearbook* **8**.
Srivastava, S. C. (1964). A new host record (*Mellivora*) for *Strongyloides akbari* and *Artytechinostomum sufrartyfex*. *Indian J. Helminth.* **16**.
St Leger, J. (1932). On mammals from north-west Damaraland South West Africa, obtained during Cpt. Shortridge's 6th Percy Sladen and Kaffarian Museum Expedition. *Proc. Zool. Soc. London.*
Steinbacher, G. (1939). Nüsse öffnender Sumpfichneumon. *Zool. Garten Lpz.* **10**.
Steinbacher, G. (1951). Nüsse öffnender Sumpfichneumon. *Zool. Garten Lpz.* **18**.
Stephens, M. N. (1957). "The Natural History of the Otter". UWAF, London.
Stephenson, (1966). *In* Tanganyika National Parks Reports.
Sterndale, H. *In* Hanström, B. (1949). *Afr. Wildl. J.* **3** (3), 203–9.
Stevenson-Hamilton, J. (1912). "Animal Life in Africa". Heinemann, London.
Stevenson-Hamilton, J. (1914). The coloration of the African hunting dog, *Lycaon pictus*. *Proc. Zool. Soc.* **1914**, 403–5.
Stevenson-Hamilton, J. (1922). *In* Shortridge, G. (1934). "The Mammals of South West Africa". Heinemann, London.
Stevenson-Hamilton, J. (1923). *In* Shortridge, G. (1934). "The Mammals of South West Africa". Heinemann, London.

Stevenson-Hamilton, J. (1929). "The low-veld: its Wild Life and its People". Cassel, London.
Stevenson-Hamilton, J. (1950). The African hunting dog. *In* "Wildlife in South Africa". Cassel, London.
Stevenson-Hamilton, J. (1954). Specimen of the extinct Cape lion. *Afr. Wildlife* **8** (3).
Stevenson-Hamilton, J. (1954). "Wildlife in South Africa". Cassel, London.
Steyn, T. (1951). The breeding of lions in captivity. *Fauna and Flora Pretoria* **2**, 37–55.
Stuckberry, H. B. (1967). Has anyone seen Stripey? *Africana* **3** (2) June.
Stubbe, M. (1969). Zur evolution der analen Markierungsorgane bei Musteliden. *Biol. Zbl.* **88**, 637.
Stubbe, M. (1970). Zur Evolution der analen Markierungsorgane bei Musteliden. *Biol. Zbl. Lpz.* **89** (2), 213–23.
Swynnerton, C. F. M. (1936). The tsetse flies of East Africa. *Trans. Roy. Ent. Soc.* **84**.
Swynnerton, G. H. (1958). Fauna of the Serengeti National Park. *Mammalia* **22**, 435–50.
Swynnerton, G. H. and Hayman, R. W. (1951). A checklist of the land mammals of the Tanganyika Territory and the Zanzibar Protectorate. *J. E. Afr. Nat. Hist. Soc.* **20**, 274–392.
Szeky, P. (1969). Comparative investigations on ontogenetic changes in body proportions of Mustelidae. *Agrartud. Egeyetem. Közlem*, 45–72.
T.G.R. Tanganyika Game Reports 1934–1946.
T.P.R. Tanganyika Park Reports 1938–1960.
Tarlton, A. *In* Roosevelt, T. (1910). "African Game Trails". New York.
Taylor, M. (1969). Notes on the breeding of two genera of viverrids, *Genetta* spp. and *Herpestes sanguineus* in Kenya. *E. Afr. Wildl. J.* **7** 168–9.
Taylor, M. (1970). Locomotion in some East African viverrids. *J. Mammal.* **51**, 42–51.
Taylor, M. (1973). The comparative anatomy of the limbs of East African Viverridae. *Dis. Abstr. Int. B. Sci. Eng.* **33** (18), 5072–3.
Taylor, W. T. and Weber, R. J. (1951). "Functional Mammalian Anatomy (with special reference to the cat). Van Nostrand, New York.
Theiler, G. (1951). The African striped weasel. *Afr. Wildlife* **5**, 168–9.
Thenius, E. (1966). Zur Stammesgeschichte der Hyänen (Carnivora Mammalia). *Z. Säugetierk.* **31**, 293–300.
Thesiger, W. (1970). Wild dog at 5894 metres. *E. Afr. Wildl. J.* **8**, 202.
Thomas, O. (1928). On the East African mongoose described as *Galeriscus jacksoni. Ann. Mag. Nat. Hist. Soc. Ser.* 10, **1**.
Thompson, D'Arcy, W. (1917). "On Growth and Form". Cambridge University Press.
Thorneycroft, G. (1958). African palm civet. *Afr. Wildlife* **12**, 81.
Thornton, D. D. (1962). Lion bay experiment Q.E.N.P. part II. Grassland ecology investigations. Unpubl. M/S Vet. Dept. Entebbe, Uganda.
Tierkel, S., Arbona, G., Rivera, A. and de Juan, A. (1952). Mongoose rabies in Puerto Rico, *Publ. Hlth. Report, Washington.*
Tomich, P. Q. (1969). Movement patterns of the mongoose in Hawaii. *J. Wildl. Mgmt.* **33**, 576–84.

Torre, D. (1967). Analisi di alcune differenze nell' apparato masticatorio dei leoni e delle pantere. *Memorie Soc. Tosc. Sci. Nat.* **74** B, 59–69.
Toschi, A. (1948). Mau mammals. *J. E. Afr. Nat. Hist. Soc.* **19**, 132–4.
Turnbull-Kemp, P. (1967). "The Leopard". Howard Timmings, Capetown.
Turner, K. (1968). How to make friends with a bat-eared fox. *Africana* **3** (6).
Turner, M. (1965). Tanzania's Serengeti. *Africana* **2** (5).
Trew, C. (1940). "The Story of the Dog". London.
Tweedale, M. S. *In* Uganda Game Department Reports for 1952.
Udvardy, M. D. F. (1969). "Dynamic Zoogeography". Van Nostrand Reinhold.
U.G.D.R. Uganda Game Department Reports 1935–1959.
Ulbrich, F. and Schmitt, J. (1969). Die Chromosomen des Erdwolfs *Proteles cristatus* Sparrman 1783. *Z. Säugetierk.* **34**, 61–2.
Ullrich, W. (1962). Die letzten indischen Löwen. *Zool. Garten Lpz.* **26**.
Ulmer, F. A. (1941). Melanism in the Felidae, with special reference to the genus *Lynx*. *J. Mammal.* **22**, 285–8.
Ulmer, F. A. (1966). Voices of the Felidae. *Int. Zoo Yearbook* **6**.
Valen, van L. (1963). Notes on the ear region of *Nandinia*. *J. Mammal.* **44**.
Valen, van L. (1964). Nature of the supernumerary molars of *Otocyon*. *J. Mammal.* **45** (2), 284–6.
Valen van L. (1969a). Evolution of dental growth and adaptation of mammalian carnivores. *Evolution Lancaster Pa.* **23**, 96–117.
Valen, van L. (1969b). The multiple origins of the placental carnivores. *Evolution* **23**, 118–30.
Vanderput, R. (1937). La civette. *Bull. Agric. Congo Belge* **28**, 135–46.
Varaday, D. (1964). "Gara Yaka. The Story of a Cheetah". Collins, London.
Verbene, G. (1970). Beobachtungen und Versuche über das Flehmen katzenartiger Raubtiere. *Z. Tierpsychol.* **27**, 807–27.
Verheyen, R. (1951). "Contribution à l'Étude Éthologique des Mammifères du Parc National de l'Upemba". Inst. Parc. Nat. Congo Belge Bruxelles.
Verschuren, J. (1958). Écologie et biologie des grands mammifères: *Explorat. Parc. Nation. Garamba Bruxelles.*
Vigne, G. T. (1842). "Travels in Kashmir etc". London.
Volf, J. (1957). À propos de la reproduction du fennec. *Mammalia* **21**, 454–5.
Volf, J. (1959). La reproduction des genettes au Zoo de Pragua. *Mammalia* **23**.
Volf, J. (1965). Trente-deux jeunes de la Genette. *Mammalia* **28**, 658–9.
Vosseler, J. (1928). Beobachtungen am Fleckenroller *Nandinia binotata* (Gray) *Z. Säugetierk.* **3**, 80–91.
Walker, E. P. (1968). "Mammals of the World". Johns Hopkins Press, Baltimore.
Walker, L. W. (1945). *Herpestes*: history and habits in Hawaii. *Nat. Hist. N.Y.* **54** (9).
Walls, G. L. (1942). "The Vertebrate Eye and its Adaptive Radiation". Harper, New York.
Watson, M. (1950). The wild animals of Teso and Karamoja. Part V. *Uganda J.* **14**.

Watson, R. M. (1965). Observations on the behaviour of young spotted hyaena *Crocuta crocuta* in the burrow. *E. Afr. Wildl. J.* **3**, 122–3.
Webb, C. (1947). Neumann's genet. *Zoo Life, London* **2**, 108.
Weigel, I. (1961). Das Fellmuster der wildlebends Katzenarten und der Hauskatze in vergleichender und stammesgeschichtlicher Hinsicht. *Säugetierk. Mitt.* **9**, 1–120.
Wells, M. E. (1968). A comparison of the reproductive tracts of *Crocuta crocuta, Hyaena hyaena* and *Proteles cristatus*. *E. Afr. Wildl. J.* **6**, 63–70.
Wemmer, C. (1972). The behaviour of *Genetta tigrina* and related genera. Ph.D Thesis, University of Maryland College Park.
Werken, van der H. (1968). Cheetahs in captivity. *Zool. Garten Lpz.* **35**.
Wickler, W. (1965). Die Evolution von Mustern der Zeichnung und des Verhaltens. *Naturwiss.* **52**, 335–41.
Wier, J. and Davison, E. (1965). Daily occurrence of game animals at water holes during dry weather. *Zool. Africana* **1** (2), 353–68.
Wier, J. and Horsefall, F. L. (1940). The recovery from patients with acute pneumonitis of a virus causing pneumonia in the mongoose. *J. Exp. Med.* **72**, 595–610.
Wilhelm, J. H. (1933). *In* Shortridge, G. (1934). "The Mammals of South West Africa". Heinemann, London.
Wilkinson, J. G. (1878). "The Manners and Customs of the Ancient Egyptians", Vol. 3. John Murray, London.
Willoughby Lowe, G. (1932). "The trail that is Always New". Witherby, Exeter.
Wilson, V. J. (1966). Predators of the common duiker, *Sylvicapra grimmia*, in Eastern Zambia. *Arnoldia* **28** (2).
Wilson, V. J. (1968). Weights of some mammals from Eastern Zambia. *Arnoldia* **32** (3).
Wilson, V. J. (1969). The large mammals of the Matopos National Park. *Arnoldia* **13** (4).
Wilson, V. and Child, G. (1966). Notes on development and behaviour of two captive leopards. *Zool. Garten Lpz.* **32**, 67–70.
Winton de, W. E. (1902). *In* Hinton (1921a).
Woosnam, R. B. *In* Shortridge, G. (1934). "The Mammals of South West Africa". Heinemann, London.
Wright, B. S. (1960). Predation on big game in East Africa. *J. Wildl. Mgmt* **24**, 1–15.
Wüstehube, C. (1960). Beiträge zur Kenntniss besonders des Spiel und Beutverhaltens einheimischer Musteliden. *Z. Tierpsychol.* **17**.
Wyatt, A. W. (1950). The lion men of Singida. *Tanganyika Notes and Records* (28 Jan).
Wyman, J. (1967). The jackals of the Serengeti. *Animals* **10**, 79–83.
Wynne Edwards, V. (1962). "Animal Dispersion in Relation to Social Behaviour". Oliver and Boyd, Edinburgh.
York, J. F. (1973). A study of serval melanism in the Aberdares and some general behavioural information. *In* "The World's Cats" Vol. I. World Wildlife Safari, Oregon.
Zabinski. (1949). The birth of a *Lycaon pictus* in the zoological garden of Warsaw. *Bij. der Dierk* **28**, 1949.

Zannier, F. (1965). Verhaltensuntersuchungen an zwergmanguste *Helogale undulata rufula* in Zoologischen Garten Frankfurt. *Z. Tierpsychol.* **22**.

Zdanski, O. (1924). Jungtertiäre Carnivoren Chinas. *Palaeont. sin. C.* **2**(1), 1–149.

Zeuner, F. E. (1963). "A History of Domesticated Animals". Hutchinson, London.

Zukowsky, L. (1924). Beitrag zur Kenntniss der Säugetiere der nördlichen Teile Deutsche-Sudwestafrikas unter besonderer Berücksichtigung des Grosswildes. *Arch. Natg. Berlin* **90** A (1).

Zukowsky, L. (1959). Perische Panther. *Zool. Garten Lpz.* **24**.

Zyl, van J. H. (1972). *In* Du Plessis, S. S. (1972). D.Sc. Thesis, Pretoria.

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